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THE STEM-NODE-LEAF CONTINUUM OF THE DICOTYLEDONEAE

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ALTHOUGH THE STEM, the node, and the leaf are treated as individual structures in many textbooks of general botany or plant anatomy, an understanding of the internal structure of any one of these is associated with information from the adjacent structure. The stem-node-leaf is a continuum of cells and tissues. An excellent article by Wetmore and Steeves (1971) considers the continuum from the developmental point of view and was written for the physiologically oriented reader.

The present study is derived from a survey of the structure of the node and the petiole to be contributed to a new edition of Metcalfe and Chalk's *Anatomy of the Dicotyledons*. Stems and leaves of representatives of every family of the Dicotyledoneae have been examined. For each family of the Takhtajan system to be followed in the new edition of *Anatomy of the Dicotyledons* (Metcalfe 1972) a description will be given there of the patterns of vascular tissue found in the internode, the node, the petiole, and the leaf blade to its apex, as revealed in a series of sections.

The material following here is a summary of the considerations needed in order to obtain a proper interpretation of the vascular patterns seen at the various levels of the stem-node-leaf continuum.

LEAF DEVELOPMENT

The development of the foliage leaf has been considered in detail for a relatively few dicotyledons, when one considers the number of taxa recognized in the class. Yet morphologists suggest that there is a basic pattern of development which is common to leaves in general, and that the difference in final form of the mature leaf can be explained in variations on one morphogenetic theme (Wetmore & Steeves 1971).

Upon and within the apex of the stem, a primordium of a leaf is distinguishable in a definite relationship to other primordia, which is expressed eventually as the phyllotaxy of leaves on a stem. This arrangement may be established as alternate, opposite, whorled, or orixiate

(Maekawa 1948). A distichous arrangement is considered to be superimposed.

Wetmore and Steeves (1971) reviewed the experimental work that has been done on leaf primordia, and Wetmore and Garrison (1966) are among the recent authors to state that "incontrovertible evidence now exists that primordia when produced on the apex are uncommitted. It is their natural biochemical milieu which determines their developmental destiny whether leaf or bud." Surgical isolation allows young leaf primordia to appear as buds.

The leaf primordium undergoes a period of growth, establishing a foliar axis, and perhaps, by basal elongation, the stem. The existence of recognizable areas within the primordium, variously termed soubassement, leaf buttress, leaf base, Unterblatt, and Oberblatt, has been suggested by some authors and denied by others.

The axis of the foliar primordium develops an adaxial meristem responsible for the thickening of a midrib region. An apical meristematic zone of the primordium may continue temporarily the elongation of the primordium. Marginal meristems along the foliar axis develop either the lamina of a simple leaf or the leaflets of a pinnately compound leaf. Divisions at the apex of the primordium develop the leaflets of a palmately compound leaf. Multidirectional expansion of an apical meristematic area produces the ascidiate or peltate leaf blade. Subsequent intercalary growth may be responsible for the petiolar area or the regions of the rachis between blade lobes or pinnae of compound leaves. The timing and relative development of each of these meristematic potentials can explain the form and size of the ultimate leaf (Kaplan 1970a, 1970b).

During its development, meristematic activity of cells within the leaf may be restricted and finally cease, with the subsequent enlargement being caused only by increase in cell size. The dicotyledonous leaf is generally assumed to have limited terminal growth. Examples of continued apical growth have been reported in the Meliaceae (Skutch 1946), while variable development of laminar portions of the blade and the axis of simple leaves is evident in tendrils of *Mutis* spp., *Triphyllophyllum*, and interrupted blade development in *Nepenthes* and *Codiaeum*. Residual meristematic activity of other cells is evident in the production of "leaf-plantlet meristems" (Warden 1971-72) normally in *Bryophyllum* spp. and in *Tolmeia menziesii*, or in the vegetative "leaf cutting" reproduction of many Gesneriaceae, Begoniaceae, etc. Limitation of expansion of the leaf may be due, in part, to the maturation of tissues, that is, the production of xylem and the development of a cambium and secondary tissues, and even the maturation of the mesophyll cells. However, the pulvinal areas may never develop sufficient quantities of xylem tissue to be considered incapable of further elongation or meristematic development.

Vegetative propagation of dicotyledons from leaf cuttings indicates a residual meristematic potential in some herbaceous plants. No woody plants are known to be reproduced from leaf or petiole cuttings alone. *Saintpaulia*, *Begonia*, *Peperomia*, are examples of plants which can be

reproduced with ease from petiole plus blade cuttings. Reproduction from portions of the leaf blade are considered practical by the nurseryman only when they involve a portion of the midvein or a lateral vein. Regeneration is believed to come from dedifferentiation of some mature cells or from callus.

As the primordium develops into a recognizable leaf form, the vascular system is differentiated in stages, first as a procambial stage, and subsequently as xylem and phloem. The differentiation of the procambium is generally described as acropetal, taking place while the primordium is still undergoing cell division and even elongation. Differentiation of the phloem from the procambium is acropetal into the leaf primordium. Later, differentiation of xylem begins at the base of the leaf primordium and develops acropetally into the leaf and basipetally into the stem. The continuity of conducting tissue from the stem into the leaf is thus established and recognized as the primary vascular system.

In general, developmental studies have been concerned with primordia and very immature leaves. No literature seems to concern the development of the many varied and complex patterns of arrangement of mature vascular tissues in the petiole of the mature leaf, or how such complexities are established in an interpolated organ. The independence of bundle development is specified in a few ontogenetic studies. Although it appears from most studies that the median bundle extends into the developing leaf at a faster rate than lateral traces, Kaplan has shown (1970a) examples of the more rapid acropetal development of the primary lateral traces. The need for later stage developmental studies represents a serious lack of information when one considers that the leaf primordium may: interpolate a petiole; separate the rachis with or without articulations in the development of pinnate compound leaves; develop one to many pulvini; and form accessory foliage organs or appendages as stipules, stipels, thorns or glands.

THE PRIMARY VASCULAR SYSTEM

Shortly below the apical meristem of most shoots of the dicotyledons the primary body can be recognized as the vascular tissue, the pith, and the cortex. In cross sections the vascular tissue may be a continuous ring; that is, a siphonostele, or a series of discrete bundles, a eustele. Whether or not all of the vascular tissue is to be regarded as of leaf origin remains a matter of dispute. Some authors refer to the discrete bundles of the stem as traces, noting the ultimate departure of the tissue into the leaves. Other authors, noting the identity of the bundle for several internodes, refer to some bundles either as "stelar" or "cauline" bundles (Dormer 1972), thus distinguishing them from their branches or leaf traces, or as sympodia, indicating their multiple nature as branched or fused units. The primary vascular tissue can be recognized as occurring in many patterns until the development of metaxylem or secondary tissues makes the patterns obscure (Esau 1965). The patterns which have been described

as "vascular systems" are based on a study of the path of the leaf traces down the stem. Individual traces, upon association with others in the stem, may join with them in entirety or by bifurcation to establish the vascular continuity. This may occur immediately below the node or at a greater distance involving several internodes. Generally the path downward is helical and associated with a spiral phyllotaxy, but in distichous or decussate leaves the path may be straight.

The studies of "eustelic" systems have been dominant in the literature, primarily due to the ease of obtaining these from seedlings or herbaceous plants. Dormer (1945) classified the vascular systems as "open" or "closed." The closed system is essentially a reticulum or network of bundles which branch or anastomose, depending on the direction the author accepts for his terminology, to or from the leaves. The open system is characterized by bundles which branch, but only exceptionally rejoin. Dormer did recognize that there were intermediates, or that both types could occur in the same vascular system. The "branches" from either system are the traces which enter the leaves, and the vascular tissue from which the branch originated is termed a stem bundle or a sympodium.

Most authors now attempt to illustrate diagrammatically the primary vascular system by assuming that the stem could be slit along one side and flattened. The vascular system is then shown in two dimensions, and the sympodia or cauline bundles are usually illustrated as heavier lines, the traces to leaves as lighter lines. The number of sympodia may be of descriptive value (e.g., the symmetrical six-fold to symmetrical twelve-fold systems, Slade 1971), as well as the nature of the branch trace pattern as cathodic or anodic into the meshes or interstices. The diagrams show the open system as unconnected vertical paths of vascular tissue, and the closed system as a reticulum of anastomosing tissues. Opposite, decussate, distichous, alternate or whorled-leaf arrangements can be correlated with unilacunar, trilacunar, or multilacunar nodes. Cortical or medullary bundles can be superimposed on such a diagram (Balfour & Philipson 1962). The vascular supply to axillary buds or branches has been generally neglected in such studies, although Dormer (1972) illustrates by diagrams some of the patterns previously reported.

Philipson and Balfour (1963) reviewed and illustrated the primary vascular system patterns recognized to that time. Subsequently Jensen's (1968) study of the Crassulaceae, which recognized sixteen patterns within one family, indicates that the survey is far from complete.

Benzing (1967a, 1967b) studied the primary xylem of the "woody Ranales," in which a pseudosiphonostele (Bailey & Nast, 1948) is present rather than the eustele studied by other authors. In a pseudosiphonostele there is a continuous ring of procambium and primary phloem near the stem apex, but the protoxylem is circumferentially discontinuous. What appears to be a single leaf trace to a unilacunar node or the individual traces of a trilacunar node may be, in fact, one or several strands of protoxylem exhibiting both "open" and "closed" systems in a variation

of the application of those terms from that used by Dormer and others. By following the path of a protoxylem in species with unilacunar, trilacunar, and multilacunar nodes, additional diverse protoxylem strand patterns were recognized.

Benzing concluded from his evidence that the primitive node in the Angiospermae was a one-trace node (one protoxylem strand), either unilacunar or trilacunar in nature. He suggested that the two-trace unilacunar node of the *Clerodendrum* type (Marsden & Bailey 1955) is derived.

The descriptive value of the primary vascular system and/or the protoxylem patterns has been demonstrated. In the eustelic type of vascular system, the primary vascular pattern may be retained in the mature plant. In most woody plants, however, the primary vascular pattern is evident only in the upper few immature nodes and internodal portions of the shoot, due to the obscuring effect of cambial activity.

BUDS AND BRANCHES

By factors still unknown at the present time, the products of the apical meristem may be variable in regular or irregular sequences. One can consider as a unit of seasonal growth the stem and associated appendages produced during a growth interval, a season for example. The terminal bud of a temperate area woody plant extends in length until another terminal bud is formed, and this amount of growth is here termed a seasonal-unit, for Wetmore and Steeves (1971) have accepted the internode as the "growth unit." The appendages produced on this seasonal-unit may vary in size from scales such as prophylls or cataphylls, to eophylls, or to full foliage leaves. The seasonal-unit may have the smaller appendages at the base, larger ones in the middle, and either a gradual reduction in appendage size near the apex, or an abrupt reduction in size to the protective bud scales and the stem apex within the terminal bud. The mature foliage leaves may be largest at the base of the seasonal-unit, at the middle, or at the upper end.

Internodal elongation may be negligible at the base of the seasonal-unit, evident almost as in short shoots, and also at the apex of the seasonal-unit by the approximation of the foliage leaves below the terminal bud. In contrast, the basal internodes of the seasonal-unit may be greatly extended to form a hypopodium with cataphylls in great size contrast to the other nodes and internodes.

By the time a fourth leaf primordium has been differentiated at the stem apex, there may be evidence of an axillary bud in *Syringa* (Garrison 1949, Wetmore & Garrison 1966). The time of axillary bud initiation appears to vary in different taxa, although it is fairly consistent within the taxon (Wetmore & Steeves 1971). Buds are usually produced singly in the axils of foliage leaves, but they may be in multiples arranged horizontally or vertically or even extra-axillary in position. Buds may be sunken in stem tissue and covered by cortical tissue or protected by a sheath or by a concave petiole base.

The buds along a seasonal-unit may be vegetative buds or floral buds, or both may be present in the axil of a given leaf. Leaves at the basal nodes of a seasonal-unit may have the buds reduced in size, or they may be completely lacking. The production of vegetative or flower buds and the conversion of one type to the other have been demonstrated in the literature (Wetmore & Steeves 1971). No studies appear to have been made of the occurrence of both types of buds in axillary positions in many flowering plants. When two or more vertically arranged buds are present in the axil of the foliage leaf, either the upper or the lower bud alone may develop, or neither or several in apparently characteristic patterns. Thimann (1961, 1972) attributes the lack of bud formation in some nodes to the inhibiting effect of the leaves present, while the elongation of buds can be controlled by the balance between auxin and kinetin. Axillary vegetative buds may develop in a given growth period of (sylleptic) shoots, or be retarded, as in many temperate plants (proleptic), and develop only during the second year. In some genera the development of an axillary vegetative bud may be restricted by the conversion of the apex to a spine by the abrupt reduction of the apical meristem.

Flower buds are also produced in characteristic patterns of terminal, axillary, or extra-axillary positions. Within the seasonal-unit the flowers may be produced in all leaf axils, only in the lower leaf axils, at the middle, or in the upper leaf axils. If the lower leaf axils of the seasonal-unit characteristically produce the flower buds, these nodes are without vegetative branches in succeeding years, producing the appearance of separated units of leaves.

Cutter (1961) and others have noted that in some members of the Nymphaeaceae, sites in the genetic spiral have alternate developmental potentialities. Leaf and flower primordia in the same spiral may be formed consecutively on the apical meristem; that is, the physiological conditions conducive to flower formation must be followed immediately in a different sector of the apical meristem by those favoring leaf inception, and then again, flower formation. Occasionally flowers will occupy leaf positions in such a spiral. Cutter (1966) also reported the condition in many plants with opposite leaves where the vegetative and floral axillary buds occur in either sectorial or helicoidal patterns.

Wetmore et al. (1964) noted that "any of the young potential leaf primordia may become buds if isolation of the very young primordia is effected adequately soon after their appearance." These studies suggest that the original primordia are uncommitted and undifferentiated protuberances of cells as they are initiated.

The vascular supply of the axillary bud is usually associated with tissue on one or both sides of a gap within the vascular cylinder. Dormer (1972) illustrates examples of the vascular supply of the axillary bud being derived from the leaf traces themselves. In unilacunar nodes, the bud traces are associated with the single gap. In trilacunar nodes all cases reported to the present reveal the bud traces to be developed only from the central gap (Garrison 1949). Ogura (1964) reported multilacunar

nodes with vascular supply to the axillary buds developed from several of the gaps in the Araliaceae, Compositae, Plumbaginaceae, and Ranunculaceae. No literature has been located describing the vascular supply to serial buds, whether arranged vertically or horizontally. Croizat (1960) has reported a node of *Chaenomeles* in which buds or branches were formed within the axil of the foliage leaf and each of the adjacent stipules, but he gave no anatomical details. Nast and Bailey (1946), and Garrison (1949) also reported the intermingling of bud and leaf traces in *Euptelea*.

Recently Bounaga (1973) has reported experiments in which an axillary bud was excised and the portion of the stem from which the bud was removed was grown in culture media. The study involved material of *Cestrum parquii*, *Dianthus barbatus*, and *Matthiola annua*, all of which have unilacunar nodes; and *Eryngium tricuspdatum* and *Bupleurum plantagineum*, both of which have multilacunar nodes. When grown in culture, the stem pieces developed new buds at the area of excision. Buds developed with connections to vascular tissue on either side of the leaf-gap or from only one side in the unilacunar nodal types. A variable number of buds, not exceeding the number of traces, developed in the cultured material of *Eryngium* and *Bupleurum*. Bounaga concluded that the production of neobuds was "inscribed" in the bud trace, and that the stems in the taxa studied were not caulogenic.

If the growth of the apical meristem in any given season is determined by the development of a terminal bud, this bud can be a flower bud, producing an inflorescence, or a vegetative shoot. In some plants the termination of apical growth results from the gradual reduction in size of the apex meristem and its appendages to the form of a spine. Subsequent elongation of the axis occurs through the elongation of a lateral bud. Growth may also terminate by the abortion of the shoot apex, a conspicuous failure of shoot development. Apical growth may be limited, too, by cladoptosis, the abscission of a portion of the shoot, a part or all of the seasonal-unit (Garrison & Wetmore 1961).

The onset of dormancy is often indicated by the lessening of the length of the internodes, and the closer association of the upper leaves or their reduction in size. The abrupt cessation of production of leaves in a seasonal-unit, followed by the development of bud scales, must be under hormonal control. Dostal (1959) showed that the removal of shoot leaves would delay the production of bud scales and cause the production of more leaflike organs.

With the onset of new growth, either as lammas shoots or following a seasonal dormant period, the bud internodes begin to increase in length. The outer bud scales usually abscise, and internodal elongation is lacking in the area of the bud scales. Some plants evidently enlarge in a given seasonal-unit only those leaf primordia found in the resting bud. Even this development may show transitional forms characterized successively as cataphylls, eophylls, or transitional leaves and characteristic foliage leaves. Bud scales and cataphylls commonly lack petioles, and may lack

photosynthetic potential or have this reduced. Eophylls may or may not have a full petiole development comparable to that of the later leaves. The vascular supply or nodal type for each of these appendages may be different. Lammas shoots commonly have larger cataphylls and eophylls than comparable appendages developed from a true resting bud, and such appendages may be long lasting. Some plants with determinate growth and terminal buds may not only develop the leaf primordia included within the bud as "early leaves," but may continue to develop additional leaves, as "late leaves" (Critchfield 1960) before forming a terminal resting bud.

Plants with indeterminate growth, that is, those that do not form a resting terminal bud, may continue to produce standard foliage leaves until stopped by adverse weather in temperate regions. When a die back of tissue occurs, subsequent elongation of the stem takes place through the growth of an axillary bud in a lower position.

THE NODE

The node is commonly defined as the position on the stem at which leaves occur — a superficial topographic orientation. Variations within this definition allow for the node to have one leaf, two or opposite leaves, and several or whorled leaves associated with a single node.

When the leaf has abscised, a leaf-scar remains visible, commonly revealing cross sections of one or more vascular bundles, referred to as traces, which are the paths of conduction between the leaf and the vascular system of the stem. When the traces enter (or depart, depending on the point of view) the vascular system, a gap or gaps can be found in the higher plants. This area of gaps has also been accepted as a "node," permitting two contrasting considerations for descriptive purposes. The widely accepted classification, attributed to Sinnott (1914) although recognized much earlier, established three nodal types, unilacunar, trilacunar or multilacunar, depending on the number of gaps. Pant and Mehra (1964) have suggested the nodal classification of alacunar, unilacunar and multilacunar when the number of gaps is more than one. Independently in Europe emphasis was placed on the number of traces instead of the number of gaps. Pierre (1896) suggested the *Monoxylées* or *Monophalangoxylées* and the *Trixylées* or *Triphalangoxylées* for one or three traces entering the stem; while Hasselberg (1937) established the terminology "Unifaszikulärer insertion," "Trifaszikulärer insertion," and "Multifaszikulärer insertion." Later Marsden and Bailey (1955) combined the number of traces and gaps, recognizing a "fourth type of nodal anatomy" when the traces were two at one gap; and Takhtajan (1969) proposed a hypothetical but comparable "fifth type" with two traces to a median gap and single traces to each of two lateral gaps.

Arnal (1962) discussed alternative characteristics for a node, suggesting that it has been defined either as a zone of insertion on the stem of a leaf-axillary bud complex, or as the zone of non-elongation of the stem.

He acknowledged that the presence or absence of buds, including the formation of axillary and adventitious buds, was extremely variable; that leaves may be present or absent, and that internodes might also be lacking; and concluded that the only criterion for a node was that of non-elongation.

Croizat (1960), by contrast, has called attention to the variety of structures that could be produced and be present superficially in an area which he called a "nodal torus," such as buds, shoots, flowers, inflorescences, scales, cataphylls, eophylls, leaves, stipules, trichimoids, spines, glands, and meristematic tissue. He recognized that the nodal torus could occupy a considerable portion of the stem, far exceeding the leaf-scar area and the gap region of the stele. He pointed out that these products of the nodal torus are found completely surrounding the axis, sometimes extending a distance above the leaf-scar or occurring below the leaf-scar.

Boke (1961), noting that areole meristems of the Cactaceae produce new spines seasonally for many years, considers these to be dwarf shoots rather than simple buds, thus a single nodal torus.

No survey paper has yet considered, in the definition of a node, the presence of a cortical and/or medullary vascular system which may or may not contribute to the principal vascular cylinder and/or the leaf. Neither has attention been paid to accessory conducting-secreting systems as latex or resin canals and their role in the leaf-stem relationship.

Ideally all of these characteristics should be incorporated in any description of a node, but most important is the recognition of the nodal area in three dimensions. The interpretation of the single section usually drawn or illustrated is dependent on an understanding of the areas below and above that section.

The internode is generally defined as the area between two nodes, again a topographical definition. The internode is the result of both cell division and cell elongation (Wetmore & Garrison 1966), and the amount of tissue between the topographic nodes is obviously variable. If no elongation occurs and the leaves are close together, the growth form is either that of a rosette or of a short shoot. The rosette growth form is often altered with the induction of flowering and the subsequent production of internodes, especially in biennials (Wetmore & Garrison 1961). Lateral short shoots may remain as closely associated nodes for many years in flowering trees, but short shoots of terminal growth have been shown to be under hormonal control for shorter periods of time (Gunckel & Wetmore 1946, Gunckel, Thimann & Wetmore 1949, Titman & Wetmore 1955). A peculiar condition of double nodes has been reported in the genus *Anacharis* (Jacobs 1946), where occasionally an internodal area of the stem fails to elongate, and two leaf-bearing nodes are close together.

Surprisingly, the actual method of internodal elongation, with its initiation and cessation, has received little attention. Wetmore and Garrison (1961) studied the elongation of internodes in *Helianthus* and *Syringa*, and noted that in *Helianthus* elongation began at the base of the inter-

nodal area and proceeded acropetally into the supra-adjacent node, whereupon the next internode developed in a similar fashion. In *Syringa* several internodes did develop simultaneously though overlapping in timing. In *Helianthus*, cell enlargement is the dominant factor in internodal growth; whereas in *Syringa*, cell division is the more prominent of the two processes, although in both taxa mitosis and elongation are involved. In many members of the Gramineae and Liliaceae, as well as in *Equisetum*, elongation and maturation occur in the opposite direction, with the basal area of the internode the last area to mature, often remaining meristematic for some time. Although uninvestigated to the present, a similar situation may prevail in the Chloranthaceae and other plants primarily with opposite leaves, in which dried specimens show a shrunken or collapsed zone just above a pair of leaves or at the base of the internodal area. Although the processes of cell division and cell elongation are presumably under biochemical control, there is no explanation why they cease within the internodal area, causing the internode to be considered mature.

The amount of elongation, i.e. the length of the internode, may vary considerably on a given shoot or on one plant. Within a given flush of growth or development of a shoot from a bud of a woody plant, the basal portion of the stem and the apical portion may have the nodes close together, and the middle portion have the nodes well spaced. An explanation is possible if the growth hormones causing the internodal elongation are related to the appendage of the node. Thus, the lower internodes associated with bud scales, cataphylls, or eophylls are shorter than those associated with larger foliage leaves. The comparative lesser length of the upper internodes still associated with full-sized leaves immediately preceding the abrupt transition to bud scales of a terminal bud remains unexplained, as does the hypopodium development at the base of some branch systems where only cataphylls are present.

ANATOMICAL DESCRIPTION OF THE NODE

The continuity of the vascular tissue from the stem through the petiole to the apex of the leaf is evident, yet the nature of its path and the variations of pattern of bundle arrangement and position along its length have not received much consideration. A three-dimensional interpretation is desirable, yet extremely difficult to depict. Single sections in leaf-bearing regions, therefore, have generally been used to describe the node, and these remain useful. The usual single section will allow the description of the epidermis, hypodermis, and even some periderm; the cortex and its included vascular bundles in those species possessing a cortical vascular system, and sclerenchymatous tissue such as caps, rings or isolated idioblasts, and often laticiferous cells and resin cells, and the principal vascular system of secondary and/or primary phloem, cambium and secondary and/or primary xylem. The latter may be distinguishable as discrete bundles or continuous tissue being either collateral or bicollateral. The central portion of the section may be distinguishable as a pith of parenchymatous

tissue of varying size and shape, but often with complete or incomplete medullary bundles, occasionally plates of sclerenchyma, idioblasts, and canals or cells of latex or resin. In some instances the pith area may be hollow in a characteristic fashion. Needless to say, any and all of the tissues and cells may have descriptive value of a comparative nature.

The traces are generally considered to have originated in the principal vascular system, and to have "departed," leaving a gap in the vascular cylinder before entering the petiole. They may be seen in the cortical areas in cross section or in a horizontal longitudinal section. During their transit through the cortex, associated sclerenchymatous cells are usually lacking.

The descriptions of three nodal types, unilacunar, trilacunar, and multilacunar, dominate the literature (PLATE I). The fourth type of nodal structure (Marsden & Bailey 1955) indicated a condition where two traces were associated in a single gap of a unilacunar node. Nast and Bailey (1946) did not name or number the nodal condition of *Euptelea* where the bud and leaf traces were intermingled in the node, nor has such numbering been applied to the split lateral or common gap condition reviewed by Howard (1970). Takhtajan (1969) proposed a theoretical "fifth type" of nodal structure which he speculated was the primitive type, a trilacunar node with two traces in the median gap.

Added to the basic four types of nodal structures must be the stems where a cortical vascular system is present which may or may not contribute to the vascular supply of the leaf (PLATE I). This has been described for *Calycanthus*, *Chimonanthus*, and *Nyctanthes* (Lignier 1887, Fahn & Bailey 1957, Balfour & Philipson 1962, Kundu & De 1968) where the cortical system forms a girdling bundle at the node, in addition to having branches entering the leaf. Acqua (1887) illustrated but did not comment on the cortical bundles of *Buxus*. The recently described *Idiospermum australiensis*, Idiospermaceae (Blake 1972) also has a cortical system in the stem. Ogura (1937) noted that some species of *Blahdia* (*Ardisia*) of the Myrsinaceae have a cortical vascular system while others do not. A cortical system was reported for *Rhynchoptalum* (*Lobelia*) (Bower 1884) without indication of its role in the leaf vascular supply. A special study is needed of cortical vascular systems, but to the present ample material has not been available. The general pattern of the relationships of the cortical vascular system to the leaf vascular supply seems to include these variations: 1. A cortical system may run the length of the stem without association with the main vascular supply of the leaf; 2. The cortical system may run the length of the stem, giving rise to girdling branches at each node, while other branches enter the petiole; 3. The cortical system may originate just above the node and enter the leaf at the next node.

The only developmental study of cortical vascular systems appears to be that of Balfour and Philipson (1962) who studied *Chimonanthus*. They reported that the cortical system developed independently and later than the principal vascular system in the shoot apex. The cortical sympodia

are connected laterally and below the node, and each bundle gives off a branch which goes to the leaf as a lateral trace. Buds in *Chimonanthus* are vascularized both by the main system and the cortical system. One branch from each adjacent cortical bundle divides in the bud to form the two side cortical bundles of the bud vascular systems.

Medullary bundles have a varied role in their relationship to the principal vascular system of the stem and in their contributions to the vascular supply of the leaf. Metcalfe and Chalk (1950) list 55 families of dicotyledons in which cortical and/or medullary bundles are known. Lignier (1887) described the path of medullary bundles in many taxa of the Melastomataceae. Col (1904), Wilson (1924), Maheshwari (1929, 1930), Davis (1961), and Pant and Mehra (1963) all indicate the complexities of the medullary bundles in the Amaranthaceae, Chenopodiaceae, Nyctaginaceae, and Polygonaceae.

Medullary bundles may be complete bundles with xylem and phloem present, or incomplete, in which case they generally consist of phloem tissue alone. Sclerenchyma has not been found in association with medullary bundles. The medullary bundles of the Piperaceae (De Candolle 1866) may divide and anastomose with each other, and they may enter the principal vascular system of the stem or depart from it. Medullary bundles which enter the principal vascular system before entering the leaf may be indistinguishable from bundles of the usual leaf traces. In the Melastomataceae, many medullary bundles often enter the petiole independent of the bundles of the principal vascular system and retain a medullary position in the petiole (PLATE V, FIGURE 4).

In general, leaf trace bundles depart from the principal vascular system within the length of the stem that is represented superficially by the leaf base or leaf scar; i.e., the bundles make an abrupt angle. Lateral traces depart from the vascular cylinder and run horizontally around the stem in the cortex before entering the leaf. On the other hand, the traces may depart from the the vascular system a considerable distance below the leaf scar area of the stem and proceed upward in the cortex before entering the leaf. The terms cathodic and anodic traces have been applied to the traces to the left and right of the median trace; i.e., those away from or toward the direction of the spiral of the phyllotaxy. The idea of the consistent precocious departure of the cathodic trace is not substantiated. Attempts have also been made in the literature to characterize nodes of various plants on the basis of the number of bundles which are between the lateral traces or the lateral and the median trace (Record 1936). In general, the median trace is precocious in relation to the departure of the lateral traces. The fact that the traces may depart from a principal vascular system and be free in the cortex can often be determined by a superficial examination of the stem immediately below the leaf base. By far the most extreme example of early departure of a leaf trace is the example given by Johnston and Truscott (1956) of *Serjania*, where lateral traces may run in the cortex for 17 internodes before entering the leaf with the median trace.

Stems which have an opposite phyllotaxy may have the sets of traces associated with each leaf depart at the same level, or one leaf may be higher than the other in terms of trace departure. Opposite leaves may be unilacunar as to their vascular supply, or trilacunar. Opposite or whorled multilacunar nodes have not been encountered. Whorled leaves may also be unilacunar or trilacunar. Carlquist (1955) has described a member of the Compositae with whorled leaves in which traces branch and a bundle enters the base of each of the adjacent leaves. This occurrence of a split lateral or a common gap has been reported for a number of families (Howard 1970).

The presence of stipules requires a special descriptive consideration to be given later. It is possible for stipules to be vascularized by free bundles, by branches of a single lateral, or by laterals which run horizontally from their point of origin to the leaf base, fusing en route, and/or supplying branches which enter the stipules (Ozenda 1948).

Nodal sections may also give some information on the continuity of latex and resin systems between the cortex and the leaf. The number of resin canals in the internodal area or in the petiole may be several times the number of traces, but at the point of departure of the traces from the stem, only those resin canals associated with the traces persist, and the number of resin canals at the level of the abscission layer is usually equal to the number of traces (Artschweger 1943). The nature of the disappearance or the appearance of the intervening resin or latex canals has not been studied. In general, sclerenchyma caps to individual bundles will be less conspicuous in the node section than in the internodal or petiolar section.

Evidence of vascular supply to glands may also be present in the nodal section.

VARIATIONS ON NODAL PATTERNS

Sinnott (1914) considered the node as a section through the area of the leaf-trace gap, and gave a list of families of dicotyledons with unilacunar, trilacunar, or multilacunar nodes. In most cases Sinnott reported but one nodal type per family. A few corrections of interpretation and a few reports of variations have been published to Sinnott's much cited work. Sinnott considered the trilacunar node to be primitive. Subsequently Bailey (1956), Ozenda (1948), Canright (1955), Takhtajan (1969), Pant and Mehra (1964), and Benzing (1967) have arrived at differing conclusions. Trace number variation has been reported frequently in studies of seedlings where the mature nodal pattern is established three or four leaves after the cotyledonary node. Other authors have shown a variation in mature nodes of the trilacunar and multilacunar types as an inconsistency in the number of lateral traces on either side of the median trace. Kato (1966, 1967) reported such variation in *Citrus*, *Malus*, *Quercus*, and *Sorbus*, and Philipson and Philipson (1968) found a variation in *Rhododendron*.

Post (1958) studied nodes at successive levels in plants of *Swertia* and *Frasera* where traces varied from 1 to 7 per node with a comparable number of gaps. This work may be subject to some interpretation in the nature of the almost rosette-like base with the stem leaves transitional to bracts of an inflorescence. Personal studies of other Gentianaceae failed to produce the variation described by Post.

Swamy and Bailey (1949) reported a difference in the node and trace number between leaves of *Cercidiphyllum* produced on long shoots (trilacunar) and those produced on short shoots (three-trace unilacunar). Their observations cannot be repeated on material from the same tree where recent studies showed all nodes on short shoots had regular trilacunar nodes.

Variations in unilacunar nodes may be encountered when sections are not examined from a sequence of levels. The double leaf trace found in many of the cultivated herbaceous Labiatae may show a fusion of the two traces above or below the level where a double trace is evident. A third trace may be present, weakly developed between two strong traces, and may fuse with one or the other of the double-trace bundles or simply disappear (Swamy & Bailey 1950, Nakazawa 1956, Yamazaki 1965). In many herbaceous plants with a single gap, the interpretation of the number of traces is difficult when vascular development is weak. A single, broad arc-like trace may be interpreted as 2 to 5 separate bundles.

Much nodal variation was reported by Howard (1970) in the case of the split lateral traces of *Alloplectus ambiguus*. From originally wild plants the pattern was altered from a clear-cut split-lateral trace, supplying vascular tissue to opposite leaves, to a situation of two trilacunar nodes when the plants were cultivated in a greenhouse. Such material was returned to native conditions in Puerto Rico where it has since been re-examined; in all stems studied the original split-lateral trace was again present.

Slade's (1952) study of cladode anatomy in New Zealand brooms showed a variation in the number of traces in successive leaves produced in a developing seedling. The earliest leaves may have three traces from three gaps. Later leaves may have pentalacunar or septalacunar nodes, either by the occurrence of flanking traces outside of the lateral traces, or by the incidence of interpolating traces inserted between the median and the lateral traces of extremely flattened stems. A few species showed both flanking and interpolating traces. Unfortunately, this work does not show the continuity of traces through the internodes, nor are developmental studies reported.

In the course of the present study, many possible sources of variation were considered in leaves of mature stems. At an early stage in the study, 500 leaves and nodes were examined from single trees, involving crown and base leaves, sun leaves and shade leaves, those of vigorous shoots, and of short shoots or slow-growing shoots. Leaves were also obtained from single species, e.g., *Acer rubrum*, *Acer negundo*, from plants growing in states from Maine to Florida, and west to Colorado. No significant

variation was found in any instance. Many commonly cultivated tropical species, e.g., *Hibiscus rosa-sinensis*, *Lantana camara*, *Nerium oleander*, were obtained from wild material or cultivated plants from temperate area greenhouses or from botanical gardens around the world, and again vascular patterns proved to be consistent. Ecotypes were also considered, and no significant variation was encountered.

The patterns of traces and gaps accepted by Sinnott remain a good descriptive tool of anatomy and morphology. Supplemented with the accessory data on the vascular supplies of cortical and medullary bundles when these are present, a section through the node of comparable materials will yield information of descriptive value.

THE LEAF

A simple definition of a leaf proves to be a difficult exercise, due to the extreme diversity of morphology. Leaves are generally described as axillary appendages to the stem, dorsiventrally flattened, with a restricted terminal growth, an interpolated petiole, and primarily a photosynthetic function. There are many exceptions to all of these descriptive phrases. Even the relationship of the leaf to the stem remains a philosophic question, unanswered morphologically. Are the leaf and stem independent structures? Are leaves of common phylogenetic origin, or do leaves of the major taxa of the plant kingdom have diverse origins? Foster (1949) stated, and many authors have repeated the statement that "it is difficult on both theoretical as well as practical grounds to demarcate the leaf from the stem." Leaves and stems are actually integrated portions of the shoot system without sharp boundaries.

The mature leaf may be simple or compound. Pinnate and palmate compound leaves are recognized in several degrees of division and modification. Leaf blades may be entire, lobed, diplophyllous, or peltate. The distinction between a pinnately compound leaf and a pinnately lobed leaf may be extremely difficult to ascertain.

The leaf may be sessile or with a petiole of varying lengths. The leaf may have a pulvinus at the base of the petiole, and also one at the apex of the petiole. The leaf base may subtend a bud, or nearly or completely surround the bud. The base may be extended laterally and thus be sheathing in nature.

Abscission of the leaf may be by means of a layer or layers of cells developed at the base of the pulvinus, within the pulvinus, or at the apex of the pulvinus. In simple leaves the lamina may abscise, leaving the petiole to abscise later, or the whole leaf may be abscised at one time. In pinnately compound leaves the leaflets may abscise and later the petiole or rachis, or all may fall as a unit. Decompound leaves may abscise in successive parts, the ultimate divisions falling first, then successively proximate divisions, until finally the basal petiolar portion abscises from the stem. The nature of these "units" of the leaf has received little practical or theoretical consideration beyond the original definition of them by

De Candolle (1868), who classified leaves as unimerous, dimerous, trimerous, etc., to polymerous. The areas of articulation, joints or pulvini, have been noted and classified by Funcke (1929). Needless to say, the pattern of vascular tissue may be distinctive in these zones. No consideration of the pulvinus development appears in ontogenetic literature.

Although most leaves are recognized as dorsiventrally flattened, i.e., bifacial with different morphological characteristics in the cuticle, stomata, or pubescence, many examples of terete or flattened leaves have been reported and described as unifacial. A classification of unifacial leaves was proposed by Flachs (1916).

DURATION OF LEAVES

Kraus (1880) offers one of the early references to the persistence of leaves. Some conifers he reported retained their needles as long as 12 years. Dicotyledons often retained their leaves for 2 to 3 years in many species of *Ilex*, *Fagus*, and *Rhododendron*, with persistence of five years in *Buxus* and *Hakea*. Hallé (1966) reported the tropical *Schumanniophyton* with a leaf retention of 4 years, while Howard (1969) observed *Trichilia* (Meliaceae) having pinnate leaves of 4-years' duration. Pease (1917) found that the relatively smaller leaves of *Chimaphila* and *Pachystima* were retained in some cases for 8 years.

The petioles of leaves more than one year old usually show secondary xylem, with some evidence of annual increments. Attempts to estimate the volume of annual xylem production, or to correlate the amount of xylem in leaves of comparable age, were not successful.

Samantarai and Kabi (1953) observed the development of secondary xylem in the petioles of rooted leaves of *Amaranthus gangeticus*, *Chenopodium album*, and *Ipomoea batatas*. Secondary growth in *Amaranthus* was initiated outside of the original vascular bundles by accessory cambia formed in distinct arcs.

LEAF AS A CONTINUUM

There is a continuity of the vascular supply from the stem to the apex of the leaf. The nature of its variations, as revealed in transverse sections, within the length, is presented in the existing literature in a very few papers (Acqua 1887, Swamy & Bailey 1950, Nakazawa 1956, Yamazaki 1965, Schofield 1968, Sugiyama 1972).

For convenience one may consider the traces as departing from the stem and entering the leaf. The individual traces may separate ordinarily from the principal vascular system, and be seen in the cortex only immediately below the leaf gap or, in some species, in many varying numbers of internodes below the leaf gap. In the initial sub leaf-base internodal section descriptive information may include the nature and number of the traces; the presence or absence of resin canals or latex systems; the presence or absence of cortical bundles and/or medullary bundles as well as fibers or sclereids.

At the node in the classical anatomical sense, that is, the area of leaf gaps, one determines the size and nature of the traces, cathodic or anodic precocity, and the attitude or path of departure of all traces which may be on a gradual slope or abruptly at right angles to the axis. Only occasionally will traces depart from above the petiole base and curve backward, even running down the stem cortex (De Fraine 1913, Fahn 1967). Lateral traces, if present, usually run an abrupt nearly horizontal path and, when sheathing stipules are present, may produce branch traces which enter the stipular sheath.

The leaf base in the mature leaf may be of restricted development, or large and sheathing. Most leaves have a kidney-shaped scar with the axillary bud in the sinus. The leaf base may completely surround the bud, or a protuberance of unattached tissue may complete the circular protection of the axillary bud.

A pulvinus may be present at the base of the leaf and vary greatly in size and shape. Normally, the pulvinus is of greater diameter than the petiole above it. The pulvinus is regarded as an area of flexibility, as is evident in the "pouring out" leaves of tropical plants or those with nastic movements (Satter & Galston 1973). The pulvinus has a large amount of cortical tissue, a relatively small amount of vascular or supportive tissue, and appears to lack completely cambial activity or the development of sclerenchyma.

The petiole may be present or absent. If a leaf is sessile, that is, without a petiole, the basal area of the leaf often shows the same arrangement of bundles as does the pulvinus. The petiole is understood to be an area interpolated between the blade and the leaf base in development. The word pulvinus is applied arbitrarily to simple leaves as well as compound leaves. In pinnately compound leaves, the petiole is between the leaf base and the first leaflet or pair of leaflets. The remainder of the axis which bears leaflets in a pinnately compound leaf is referred to as the rachis.

In palmately compound leaves, the petiole is between the leaf base and the area of origin of the leaflets. Leaflets of pinnately or palmately compound leaves may have petiolules.

Transverse sections, taken successively from the base of the petiole to its apex, reveal the variations in number, position, and arrangement of the traces (PLATES II-VII). The lower end of the petiole is supplied with a characteristic number of traces, but successive sections reveal that these may remain independent, fuse, divide, or be rearranged, with changes in orientation. The petiole vasculature is most complex at the geographic middle of the petiole where there is the greatest amount of secondary tissue if a cambium has developed, and the greatest amount of collenchyma or sclerenchyma in the cortex and the pith of the petiole. Near the upper end of the petiole, the vascular pattern which has developed from the basal orientation may be undone in an exact reversal of its formation. Thus, in some simple leaves an upper pulvinus is present with a vascular pattern comparable to that of the lower pulvinus. In other leaves with-

out an upper pulvinus, the vascular pattern of the petiole continues into the midrib until interrupted by the departure of primary veins.

Dormer (1972) concluded that a common feature of leaves in which separate strands exist in the petiole is that these should be linked by a massive collar or bridge of vascular tissue in the leaf base. This collar is often situated at the upper end of a stipular or sheathing region. He added that "in many compound leaves a similar type of cross connection may be associated with the attachment of each pinna."

Palmately compound leaves usually have such a plexus of tissues at the apex of the petiole, and it appears that each petiolule receives a supply of vascular tissue from each of the original traces. Palmately compound leaves have been associated with unilacunar, trilacunar, or multilacunar nodes.

Peltate leaves may have a relatively simple vascular pattern at the apex of the petiole, or one of great complexity.

Within the base of the leaf blade, the vascular pattern of the midrib is re-established in complexity if the petiole pattern was simplified in the upper pulvinus. The pattern of vascular tissues in the midrib is interrupted by the departure of the primary veins in a palmate or pinnate fashion.

The distinctions between deeply lobed leaves and pinnately compound or palmately compound leaves are arbitrary. Normally, if a leaflet is attenuated at the base to a petiolule which develops an abscission layer, the leaf is considered as compound. Compound leaves may be associated with unilacunar nodes, although most appear to be associated with trilacunar nodes. In general, a leaflet of a pinnately compound leaf receives its vascular supply from branches of the median and one lateral trace.

Diplophyllous leaves may vary considerably in the amount of vascular tissue which enters the secondary laminae.

The amount of vascular tissue in the midrib of the leaf or leaflet is greatest at the base of the blade, and is progressively diminished as veins are produced. Normally, some vascular tissue, usually from the median trace, continues to the ultimate apex of the leaf blade. In some pinnately compound leaves the ultimate terminal leaflet may abort, yet a vascular supply is evident in the rudiment. The mucro of the fused leaflets of *Bauhinia* is vascularized by the median trace.

THE PETIOLE

The petiole is interpolated in the development of the leaf. Studies of its elongation are relatively few. Masuda (1933) studied this extension in woody and herbaceous plants in the botanical garden at Tokyo. He divided young petioles into equal portions with India ink marks, and followed the elongation of each section. Three types of patterns of elongation were revealed in his studies, but no attention was given to the leaf base or the pulvinal areas. Type "a" had each zone elongate almost

equally. In type "b" the upper zone of the petiole showed a conspicuous elongation; and in type "c" the lower zone showed a greater amount of elongation. Most of the study was made in May or June, although one report is for a study conducted during October. Growth was completed in as few as 6 days, or over a period of 51 days. Type "b" was regarded as the most common type with elongation ceasing from the base upward in a time sequence. Tchoun (1923) has shown that the petiole in the majority of plants completes its elongation before the lamina reaches its maximum size.

Studies were made in Boston, Massachusetts, of woody plants in the Arnold Arboretum, and revealed additional growth patterns that cannot be associated with the data given by Masuda. Using plants growing out of doors, young petioles were marked as closely as possible with India ink from the axil of the leaf base to the base of the lamina. With the exception of *Liriodendron tulipifera*, all leaves completed the elongation of the petiole in a period of 12 to 15 days. In general, the petioles appeared to increase in length in such a way that the middle of the total length of the petiole increased fastest in length and stopped its growth earliest. The expansion and cessation proceeded in a wave from the middle of the petiole to each end. The apex of the petiole, especially if a pulvinus was present, and the base of the petiole increase in length the least or not at all. *Liriodendron tulipifera* in the Boston area continues to produce leaves until growth and development are stopped by frost. The upper quarter of the petiole seemed to continue elongation as in the type "b" described by Masuda for *Liriodendron* and *Firmiana*.

The geographical middle of the petiole of leaves of most plants in the Boston area appears to increase in size first and reach maturity the earliest. This is shown internally by the amount of lignified tissue revealed by a phloroglucinol stain. A cambium may develop first at the middle of the petiole, and sequentially toward each end, being absent in the pulvinus areas. Comparable developmental patterns of sclerenchyma were observed. The pulvinal areas show the least elongation and no development of secondary tissues or of sclerenchyma.

Further support for Masuda's type "b" may be found in the statement of Funcke (1929) that some petioles are able, if necessary, to elongate themselves even after the adult stage is reached. Yin (1941) recorded growth in the length of the petioles of *Carica papaya* associated with diurnal movements of the leaves from a flexed to an upright position. The petiole was shown to grow on the lower side during the morning hours, and on the upper side during the evening hours, thus changing the attitude or position of the leaves.

Within a seasonal-unit such as occurs in a temperate tree, the lowest leaves may have shorter petioles than those of the middle of the growth unit, and the upper leaves may also have petioles comparatively reduced in length. Anisophylly of leaves and of petioles of many plants with decussate leaves has been reported by Heinricher (1910), Cook (1911), Sinnott and Durham (1923), and Howard (1970). Thus in most species

of *Acer*, the leaves borne in the horizontal plane have petioles of equal length, but those of the vertical pair have a longer petiole in the lower leaf than in the upper leaf of the pair. Anisophylly of opposite leaves in such families as the Gesneriaceae and Urticaceae is characteristic of the family and reveals leaves and petioles of different sizes in the pair. No structural differences between the leaves or in the petioles of such plants have been reported. Leaves of two different morphological forms have been reported for single plants as heterophylly. Transitions from juvenile leaves to mature leaves may be gradual or abrupt. There appear to be no differences in the anatomical structure of such variants.

Superficial observations on the petiole are of descriptive and taxonomic value. These may include the length, color, presence or absence of upper and lower pulvini, presence or absence of stipules, glands, thorns, collators, pubescence, etc. The adaxial surface of the petiole may be grooved for various distances, and the petiole may be slightly ridged to strongly winged along the groove. Sections of the petiole reveal a characteristic outline which will vary from the base to the apex of the petiole.

DESCRIPTIONS OF VASCULAR PATTERNS IN THE PETIOLE

The earliest known recognition that a section of a petiole would reveal different patterns of vascular bundles was made by Grew in 1675 when he illustrated ten schematic cross sections of petioles.

In 1868 De Candolle had proposed a theory of a leaf, likening the structure to that of a stem. The first comprehensive survey of petiole anatomy was that published by Casimir de Candolle in 1879. His survey of twenty "families" led him to describe several fundamental concepts of the vascular structure he encountered. De Candolle proposed the terminology of an open system (*système ouvert*) versus a closed system (*système fermé*). In the open system the bundles, as seen in cross section, were arranged in an arc. In the closed system the bundles formed a circle comparable to that of the stem. The bundles could be free or united. The system was invariably open at the base of the petiole, and could become closed in the petiole and again open in the midrib or in the petiolule of a leaflet. De Candolle also recognized a principal system (*système principal, système essentiel*), and an accessory system (*faisceaux détachés*), the latter composed of "*faisceaux intracorticaux*" and/or "*faisceaux intramédullaires*." The medullary bundles could have the same orientation as those of the principal system or be inverted. It should be noted that the cortical and medullary systems of De Candolle referred to the petiole alone, and were not correlated with such systems or bundles in the stem. De Candolle classified the bundle arrangement in the families he studied. He noted that groups of species in *Acer*, *Alnus*, *Aesculus*, *Mallotus* and others might have one system or the other. His division of species of *Fagus*, for example, would today represent the differences between *Fagus* and *Nothofagus*. Noting the variation in pattern encountered in a series of sections from the base of the petiole to the apex of the blade, De Candolle suggested that the most reliable comparative section could be obtained at

the first "meriphylle," that is, the interval of the midrib between the departure of the first and second primary veins.

In the decade that followed, Vesque (1885), Petit (1886, 1887, 1889), Lignier (1888) and Acqua (1887-88) added examples, ideas, and variations in terminology to the knowledge of petiole vascular patterns.

Vesque (1881, 1885) appears to be the first worker to suggest that the most reliable single section for comparative purposes be taken from the middle of the petiole. He studied a number of families and used the petiole anatomy to separate genera and families formerly united.

Petit (1886), working in France, and Acqua (1887), working in Italy, conducted broad studies of petiole vascular patterns and published their studies competitively. Petit's study involved five hundred species in three hundred genera of forty-eight families. He recognized differences in patterns along the length of the petiole and stated: "it is in a terminal section that there will be presented for each plant the disposition most complicated and most regular which offers from one plant to another the greatest differences. It is, of consequence, the section most instructive. I have given this the name of the characteristic, for in many cases it will be sufficient, in order to recognize the family of the plants, and in some cases, its genus." The names "coupe initiale" for the basal section and "coupe caractéristique" for the apical section are attributable to Petit. His work included as a resumé a key to the principal families of dicotyledons he studied on the basis of petiole vascular structure. Petit proposed a variation on the use of "open" and "closed" systems from that suggested by De Candolle. To Petit a closed system was one in which the bundles were fused; and an open system, one in which the bundles were distinct or separated. Petit felt that herbaceous plants showed distinct bundles (open) in the "coupe caractéristique," while in shrubby or woody plants the bundles were fused (closed) in an arc or a ring. He noted that sclerenchyma was generally lacking in herbaceous plants and present in woody plants, and placed value for classification on this tissue.

Acqua's study was published in full before Petit's, but following Petit's brief note indicating what he was doing. Acqua studied 19 families and proposed a classification of 13 patterns of vascular distribution in petioles. He correlated the position of the leaves with the vascular patterns; recognized unilacunar, trilacunar, pentalacunar, septalacunar, and nodes with a variable but greater number of bundles. His unit number 2 was the double leaf trace of *Phlomis* and *Lamium*, later described as the fourth type of nodal anatomy by Marsden and Bailey. Acqua also found in the Compositae examples of bundles from opposite leaves being associated with a single node, the "split lateral" or "common gap" (Howard 1970).

Lignier (1887) published an extensive monograph describing the stem, petiole, and leaf vasculature in the Calycanthaceae, Melastomataceae, and Myrtaceae where cortical and medullary bundles of the stem are involved in the vascular supply to the leaf. Three-dimensional drawings are used, and the complexities of the vascular system are described in detail. This was followed in 1888 by an essay on the vascular system of the leaf and

the stem of the phanerogams. Lignier stressed the fact that a single section of the petiole was inadequate for an understanding of the complex pattern developed in the length of the petiole. He felt that the most common pattern to be found in petioles was the arrangement of the bundles in a vascular arc. This arc could be a single broad bundle or several bundles. The arc could be expanded or divided, with extra bundles appearing at the ends of the arc. He designated the extra bundles as "surnumeraires" which were called "surnumeraires intérieurs" if they assumed a medullary position, and "surnumeraires extérieurs" if they assumed a position in the cortex of the petiole. He noted that these corresponded only in some cases to comparable terms used by De Candolle.

Lignier proposed the idea that as the vascular arc increased in size within the petiole, it would be forced into folds (plis) as the animal brain is convoluted to increase the surface area. Folds could be to the interior (pli interne) or the exterior (pli externe), and if portions were separated from the vascular arc, these would be medullary or cortical bundles of the petiole. If the vascular arc had been a complete circle, and if an arc was cut off, by foldings, toward the adaxial side, one or more vascular crowns would be recognized. Foldings with the separation of portions of vascular tissue could be recognized at the secondary and tertiary level.

Morvillez (1919) accepted the idea of foldings as a descriptive approach in his study of petiole vascular patterns. He referred to the vascular bundle pattern seen in a cross section of the petiole as a "chaîne foliaire" which could be a continuous arc of tissue or composed of separate bundles. As the arc curved inward at the adaxial ends, a crosier could be formed, and if portions of the crosier became isolated, internal bundles or plates of tissue were established in a medullary position. Dehay (1935 et seq.) and his students have used this descriptive vocabulary. Dehay chose for his illustrations the "section basilaire de la nervure médiane."

An extensive survey of vascular structure of the petiole and the leaf has been published by Watari (1934, 1936, 1939) for the Leguminosae, *Acer*, and the Saxifragaceae. Watari considered the entire length of the vascular tissue from the node through the petiole and the lamina. His detailed work concerned the many branchings of the traces and their interconnections, and is presented with sectional diagrams and complex three-dimensional reconstructions. For each group Watari proposed a classification based on the petiole structure.

Hare (1943), in a symposium on the taxonomic value of anatomical characteristics, proposed a simple classification of the vascular structure of the petioles as U-shaped, I-shaped, or O-shaped, the latter being the hollow cylinder of the petiolar vascular system. Hare related the structure to the mechanical stress of the weight of the lamina and the lateral movements of the leaf, and thought that the distinctive features of patterns should be regarded as mainly adaptive and functional, and of little phylogenetic significance. He concluded that "characters derived from the petiole, therefore, can be used with confidence, but their value for pur-

poses of classification varies widely at different taxonomic levels." The proposals of Hare were incorporated in the first edition of the *Anatomy of the Dicotyledons* (Metcalfe & Chalk 1950) as 12 diagrammatic outlines.

Howard (1963) proposed a preliminary classification relating the nodal structure at the level of the leaf gaps to the vascular patterns obtained in the petiole as follows:

Node 1-1, simple trace, flat, slightly curved or "U"-shaped.

1. Trace continuous:
 - a. Without rib traces — *Allamanda* (PLATE II, FIGURE 1a).
 - b. With rib traces — *Graptophyllum* (PLATE II, FIGURE 1b).
 - c. Trace split longitudinally, later fusing — *Eugenia* (PLATE II, FIGURE 1c).
2. Trace forming open or closed siphonostele:
 - a. Vascular system open, with terminal rib traces — *Ilex* (PLATE II, FIGURE 1d).
 - b. Vascular system open with lateral rib traces — *Actinidia* (PLATE II, FIGURE 1e).
 - c. Vascular system open, without rib traces — *Celastrus* (PLATE II, FIGURE 1f).
 - d. Vascular system closed, without rib traces — *Terminalia* (PLATE II, FIGURE 1g).
3. Trace invaginating at ends:
 - a. Ends inroll — *Lyonia* (PLATE II, FIGURE 1h).
 - b. Forming siphonostele with medullary plate — *Cordia* (PLATE II, FIGURE 1i).
 - c. Inverted plate or simple arc — *Capparis* (PLATE II, FIGURE 1j).

Node 2 or more traces from one gap.

1. Trace bipartite:
 - a. In petiole — *Clerodendron* (PLATE II, FIGURE 2a).
 - b. Below petiole — *Calycanthus* (PLATE II, FIGURE 2b).
2. Trace tripartite or more:
 - a. Bundles free, forming an arc — *Bougainvillea* (PLATE II, FIGURE 2c).
 - b. Bundles fused in an arc — *Solandra* (PLATE II, FIGURE 2d).
 - c. Bundles free, in ring — *Hernandia* (PLATE II, FIGURE 2e).

Node 3-3, bundles free.

1. Three bundles throughout the petiole — *Pedilanthus* (PLATE III, FIGURE 3a).
2. Lateral traces divide:
 - a. Petiole with five free traces — *Pittosporum* (PLATE III, FIGURE 3b).
 - b. Petiole with many traces in "U"-shaped pattern — *Miconia* (PLATE III, FIGURE 3c).
 - c. Free traces in a ring with medullary bundles — *Aesculus* (PLATE III, FIGURE 3d).
 - d. Free traces in a ring without medullary bundles — *Sambucus* (PLATE III, FIGURE 3e).
3. Median trace divides and the division products assume a dorsal position — *Hibiscus* (PLATE III, FIGURE 3f).

Node 3-3, bundles fuse to form an arc.

1. Bundles fuse and form an arc, flat or variously curved — *Lonicera*, *Betula* (PLATE III, FIGURE 3g).
2. Bundles fuse and form a flat arc with dorsal free traces — *Cornus* (PLATE III, FIGURE 3h).
3. Bundles fuse and invaginate at ends — *Congea* (PLATE III, FIGURE 3i).

Node 3-3, bundles fuse to form a siphonostele.

1. Vascular system simple:
 - a. Formed by the simple fusion of traces — *Cotinus* (PLATE III, FIGURE 3j).
 - b. Formed subsequent to division of the median, the branches of which form dorsal bundles — *Acer* (PLATE III, FIGURE 3k).
2. Vascular system with accessory bundles:
 - a. One accessory large bundle situated dorsally — *Hamamelis* (PLATE III, FIGURE 3l).
 - b. Small multiple accessory bundles dorsal in position — *Carya* (PLATE III, FIGURE 3m).
 - c. Accessory bundles in medullary position — *Bauhinia* (PLATE III, FIGURE 3n).

Node 3-3, bundles fuse to form more complex patterns.

1. By invagination forming one or many medullary bundles or plates — *Quercus*, *Tilia* (PLATE IV, FIGURE 4a).
2. Siphonostele invaginating forming included or dorsal accessory bundles — *Fagus* (PLATE IV, FIGURE 4b).
3. Siphonostele formed, then lateral invaginations giving rise to dorsal, smaller siphonostele or plate over "U"-shaped arc — *Carpinus* (PLATE IV, FIGURE 4c).
4. Polystelic types:
 - a. Axillary bud included, petiole not compressed — *Platanus* type.
 - b. Axillary bud not included, petiole compressed — *Populus* type (PLATE IV, FIGURE 4d).

Nodes multilacunar, many traces from equal number of gaps.

1. Traces remain free:
 - a. Bundles form ring or "U" — *Ricinus* (PLATE IV, FIGURE 5a).
 - b. Bundle pattern invaginates — *Rhizophora* (PLATE IV, FIGURE 5b).
 - c. By anastomosis forming concentric rings — *Coccoloba* (PLATE IV, FIGURE 5c).
2. Traces fuse:
 - a. Ring simple — *Dendropanax* (PLATE IV, FIGURE 5d).
 - b. Ring with included bundles — *Macaranga* (PLATE IV, FIGURE 5e).

Subsequent work has shown that this classification covers the majority of vascular system patterns found in the dicotyledons, but not all of the possible combinations with other characteristics. Variations have been found in genera suggesting that the use of family or generic names for the various patterns is not desirable, and the use of serial numbers would soon become unwieldy. Even the terminology used presents difficulties. In a single section the vascular tissue of a petiole may exhibit a com-

plete cylinder, but this is not a eustele at that level, nor a siphonostele in relation to other sections. Invagination and inrolling are terms of motion visually descriptive, but confusing if considered developmentally.

Although previous workers have differed in their opinions on the taxonomic value of the anatomy of the node and the petiole in the recognition of taxa, it is possible to use a combination of characteristics to devise a key to sterile material of a local flora and probably to families and genera of dicotyledons. Such a dichotomous key would involve a great many characteristics, and some of these would be repeated in several categories. For example, a simple flat arc in the petiole might arise from a unilacunar node or a trilacunar node, while the relatively simple "U"-shaped pattern of vascular tissue in the middle of a petiole could be associated with a unilacunar, trilacunar, or multilacunar node (PLATES II-IV). The same characteristics are involved in compiling a description of the vascular system extending from the internode to the leaf tip.

The following characteristics are a few of many that would be useful descriptively:

INTERNODAL AREA: Cortical or medullary bundles present or absent.

NODAL AREA PER LEAF: Leaf gaps one (unilacunar), three (trilacunar), or five or more (multilacunar) with additional consideration to the number of traces in each gap as represented either by protoxylem strands or metaxylem.

LEAF POSITION: Opposite, alternate, orixiate, whorled; distichous or decussate.

LEAF FORM: Simple, compound including sub-units for pinnate or palmate with bi- or tri-compound as well as unifoliate types. Leaves entire or lobed. Venation equally pinnate or pli-nerved or palmately veined.

STIPULES: Present or absent; type and position.

PULVINUS: Present at the base or apex of the petiole, or both, or neither.

PETIOLE: Length; characteristics such as terete, flattened, grooved, winged, or decurrent.

PETIOLE STRUCTURE: Basal or apical vascular cross-zone networks present or absent. Traces free or united; branched or unbranched, reticulate equally or unequally. Bundles collateral or bicollateral, complete or incomplete. Traces in arc, ring, with accessory bundles to the petiole stele as rib bundles adaxial plate or stele; or as medullary bundles.

A great many individual papers over the years have illustrated the vascular pattern of the petiole by diagrams, camera lucida drawings, or photographs. In interpreting any one of these publications, it is necessary to determine where the section was taken; i.e., as a "coupe initiale," the middle of the petiole, a "coupe caractéristique," or a section in the "meriphylle."

When diagrams are given indicating the relationship of the vascular bundles, the method of indicating various traces is fairly standard with variations only in the language or abbreviation used. Thus, traces seen in cross section are usually distinguished as median, lateral, and ventral, and commonly indicated as M for the median and M¹ for branches of the median; L, Lg or Ld for the laterals as "gauche" or "droit" with branches of the laterals being L1, L2, L3, etc. Bundles in an adaxial position rel-

ative to the median and laterals may be designated as A, Ad, or V (ventral) without specific reference to their origin, which may be from independent gaps as distant laterals, as branches of the median, or of the laterals.

THE ROLE OF THE TRACES

In most herbaceous dicotyledons and in some families considered woody (Euphorbiaceae, Urticaceae, Saxifragaceae, Ranunculaceae) the principal traces which enter the base of the petiole remain distinct until they reach the blade. Interconnecting branching may be present but is minimal. Even when the individual traces are broadened by the development of a cambium and the addition of secondary tissue, careful observation of the points of primary xylem will permit the identification of the traces.

In general, the median trace is either unbranched in the petiole or may produce branches which move to a medullary or adaxial position, the latter remaining free, or fusing to form a single adaxial trace, or being incorporated in the vascular ring of the petiole. The median trace of a trilacunar or higher type of node does not generally contribute to the vascularization of veins of the lower part of the blade. Often the median trace and its adaxial branches may extend and be recognized to the apex of the lamina (Sugiyama 1972).

In a trilacunar node the lateral traces may remain independent of the median trace or become intimately associated with it. If the median trace formed branches which are seen in an adaxial position, the lateral traces will be interpolated into the interstices of the vascular pattern formed by the median trace (PLATE III, FIGURE 3k). In a trilacunar node of a plant having stipules, the lateral traces may enter the stipules or supply only a branch which enters the stipules. Within the lamina the lateral traces tend to supply the vascular tissue of the basal veins, the basal lobes, or the vascular system from $1/3$ to $2/3$ of the basal portion of the lamina, while the median trace supplies all of the vascular tissue of the upper portion of the lamina. In pentalacunar or septalacunar nodes the outer lateral traces supply the lower veins or the lower lobes of the lamina successively.

Although the median trace is usually the dominant trace in the petiole, it may also be the first eliminated. Swamy and Bailey (1950), Nakazawa (1956), and Yamazaki (1965) describe the median trace in *Sarcandra* and *Chloranthus* as an unbranched trace which becomes progressively indistinct in the costa and ultimately disappears before reaching the apex. Yamazaki (1965) pointed out that in *Liriodendron* the median trace had little relationship to the lateral venation of the leaf. Bailey and Swamy (1949) described a double trace condition in the petiole and blade of *Austrobaileya*. The traces originated from different parts of the "eustele" and remained independent to the apex of the blade. Each bundle supplied lateral branches as veins for the leaf. *Trimenia* (Money et al. 1950) also had a double trace in the petiole, while *Piptocalyx* (Monimiaceae) exhibited two traces at one gap and four at the other of a pair of opposite

leaves. The two middle traces of the four fused so that the leaf received three traces. In *Ascarina* of the Chloranthaceae (Swamy 1953), two traces occur at the base of the petiole and remain distinct for most of the length of the leaf blade. The two traces present in the gap area of *Clerodendrum* (Marsden & Bailey 1955) divide in the petiole several times, and the middle ones fuse to form a single strand within the blade.

Some attention has been given by various authors to the orientation of the bundles within the petiole and the leaf blade. In general, the position of the phloem relative to the xylem, i.e., peripheral or toward the center, is of little value in single sections of the petiole. In a series of sections the changes in orientation are successive, so that a bundle with normal phloem orientation can be reversed in position a few sections later. The bundles obviously do not twist in development, but the position of the xylem and the phloem results from special paths of differentiation of these tissues in the procambial state.

In multilacunar nodes the distant trace or traces may enter only the sheathing stipules, contributing nothing to the petiole or the leaf blade, or may enter the edges of the sheathing leaf base.

METHODS OF STUDY OF PETIOLE ANATOMY

The vascular pattern of the petiole is of value as a taxonomic character useful in the identification of taxa. The systematic level of the taxonomic value does vary from one taxon to another. In some cases families can be recognized; in other cases genera, species, or varieties can be distinguished on the basis of the petiole vascular patterns.

The second edition of Metcalfe and Chalk's *Anatomy of the Dicotyledons* will contain descriptive information of petiole vascular patterns, and illustrations of these for all of the families recognized. Most of the patterns have been obtained from fresh material or material collected and preserved in alcohol.

To obtain the vascular pattern in three dimensions, a mature leaf is selected, and sections are made progressively from the internode and then through the node, the petiole, and the blade. The first series of sections taken at random intervals along the axis will determine where the critical areas of pattern change occur, although these can be expected at the node, immediately above the basal pulvinus, at the upper pulvinus or the base of the blade, at the point of attachment of leaflets, or at the departure of veins. Sections can be cut freehand with a straight razor or a single-edged razor blade, and stained in phloroglucinol and hydrochloric acid. This temporary stain does not work well on material preserved in any amount of formalin including FAA. No permanent slides are obtained by this method.

Phloroglucin stains lignified tissues, but often does so differentially. Srivastava (1966) has indicated the nature of the variation of this staining. Some plants such as members of the Thymelaeaceae assume a weak coloration with phloroglucinol or none at all.

In many cases neither fresh nor preserved material was available, and

herbarium specimens were used. This obviously restricted the amount of material available for study, and required critical initial sectioning. The herbarium material was softened in boiling water or by soaking in sodium hydroxide. Woody portions often required softening in hydrofluoric acid. The standard technique of embedding, sectioning, and staining for permanent slides was also employed, especially for material difficult to obtain, to process by hand, or to interpret. Occasionally longitudinal sections are necessary for one or several angles of approach. Clearing and selective staining methods were also used.

Although this work has been in progress for twenty years and has involved a great many technicians, the number of species studied has been a relatively small proportion of the dicotyledons. I do appreciate the assistance of many people in preparing nodal-petiole patterns, and of many individuals who supplied material; and also the cooperation of innumerable directors and curators of botanical gardens and herbaria, who gave permission for me to obtain living material or fragments from herbarium specimens.

More problems are evident in the data presented. Hopefully, individuals with access to abundant material and with sufficient time will undertake the clarification of such problems. For all who attempt to use this type of information, I can only stress again the need to visualize in three dimensions what is illustrated most frequently in only two.

STIPULES

Although the presence or absence of the stipules, as well as their form, has long been used as a diagnostic character in plant taxonomy, the morphological nature and the origin of the stipule remain obscure. The stipule is commonly defined as an appendage or pair of appendages at the base of the leaf. The stipules may be paired or single, equal or unequal in size, large, foliaceous, and persistent or reduced to a mere protuberance or a small, readily deciduous scale. Some stipules have been modified to thorns or tendrils. Stipules are often represented as a stipular sheath, and may be below the point of attachment of the leaf, well above the point of attachment of the leaf, associated with the leaf, or free from it, being axillary (Philipson 1968) to the leaf, on both sides of the leaf attached to the stem, opposite the leaf, or at varying levels of the pulvinus or the petiole. Sinnott and Bailey (1914) believed that the stipules were primarily associated with trilacunar nodes, and many authors have indicated that most stipules are vascularized from the lateral traces of a trilacunar node.

A fundamental question, unresolved to the present, is whether the stipules are part of the leaf, or independent structures. Guédès (1972) apparently believes the stipules are comparable to portions of the leaf blade or leaflets, for he stated: "a petiole generally occurs because of intense intercalary growth either below the lowest pair of leaflets and the leaf is exstipulate or between the first pair of leaflets from below and the second

one. The lower pair (of leaflets) is then isolated near the leaf insertion and becomes a pair of protostipules. It rises to the state of true stipules when proleptic development is obtained. . . . The petiole can also develop above several pairs of leaflets and there are then several pairs of stipules."

Regel (1843), Agardh (1850), Clos (1879), and Tyler (1897) have all suggested the independence of stipules from the foliage leaf in nature as well as in development. More recently Croizat (1940) proposed that the two stipules are basic structures, and between them a "dab" of meristem is found. Croizat refers to this meristem as a primary nerving center which may develop into a foliage leaf.

Examples of the seemingly independent development of stipules and the foliar leaf are many. A shoot developing from a dormant bud may produce successively cataphylls, lobed stipule-like structures, similar lobed structures with a nonpetioled lamina, and finally a normal petiolate leaf with basal stipules (Furuya 1953). Many authors have used the illustration of *Ribes* showing the retarded development of the leaf blade in successive stem appendages. Here the bud scales are clearly stipules, with the petiole and abortive leaf blade represented by a ridge, or a ridge and a small appendage. Fahn (1967, p. 194) gives an illustration of bud scales of *Vitis vinifera* where each pair of stipular scales has an included leaf. Large stipules with a rudiment of a leaf attached protect the buds in species of *Magnolia*. Large foliaceous stipules are often precociously developed in the Leguminosae. The seasonal growth of *Ilex laevigata* ends abruptly in transition from the normal foliage leaves with two minute gland-like basal stipules to an organ of three structures, the outer two comparable in size and shape to the stipules of the preceding leaf, and the middle one no larger in size and of the same shape, but in theory the primordium of the foliage leaf.

Traces which vascularize the stipules may be the complete lateral traces (Furuya 1953) or branches of the lateral traces of a trilacunar node (Bailey & Sinnott 1914). When the leaves are opposite at the node, e.g., in many Rubiaceae, the stipules of adjoining sides of the opposite leaves may be variously united, sometimes with a bifid apex or tapering to a single point (Howard 1970). The vascular supply to these conspicuous interpetiolar stipules may come from the sides of the single arc-like trace of each leaf. The branch bundles run horizontally or at an angle into the stipules, and may remain independent. In multilacunar nodes the leaf may be vascularized primarily by the centrally located vascular bundles, with small traces departing from the lateral nodes, running horizontally to the leaf base while giving rise to vertical bundles which vascularize the stipules. In some sheathing stipules (Ozenda 1948, Sugiyama 1972), the bundle or bundles most distant from the median trace may enter the stipules without connections with other bundles or with the leaf itself (PLATE I, FIGURE 1i). Sugiyama (1972) reports the bundle opposite the median trace in *Magnolia virginiana* may branch while remaining free and be noncontributory to the leaf itself.

The bundles of stipular sheaths which are above and free from the leaf,

as in *Platanus*, may be vascularized by traces completely unassociated with any vascular supply to the leaf. So, too, with stipules which are borne on the side of the stem opposite the leaf scar (*Ricinus*), or borne below the leaf (Cunoniaceae).

GLANDS

The presence and nature of foliar glands has been recognized as a useful taxonomic character (Gregory 1915, Dorsey & Weiss 1920). Zimmerman (1932) has given an extensive systematic survey and classification of extra-floral nectaries. Schnell, Cusset, and Quenum (1963) also supplied a broad survey of foliar glands with a classification, with suggestions on the phylogenetic origin of glands, and with some anatomical details.

Glands can occur on the pulvinus, stipules, petiole, or blade in various positions. They can be sessile or stalked, and with or without vascular tissue. Bernhard (1964) found the petiolar glands in certain Euphorbiaceae to be present in the primordium, and compared the glands to other lobes of the lamina. Dorsey and Weiss (1920) also considered the gland to be the equivalent of a portion of the blade, and Messager (1886) earlier had proposed the origin of the gland as an abortive laminar structure. Schnell and Cusset (1963) regard the glands as nonfoliarized "elements foliaires," or the homologues of lobes of the lamina. Cusset (1965) later proposed the term "metamere" for the "article foliaire" in a connotation differing from that used earlier by De Candolle. He suggested the primitive leaf was a single metamere glandularized at the apex, while the foliar leaf of most plants is to be regarded as a compound product of several metameres with the glands persisting or lost in the evolutionary process.

The petiolar glands may be associated with simple or complex petiolar vascular patterns arising from unilacunar or trilacunar nodes. The majority of vascularized glands receive their vascular supply from the lateral traces or their derivatives, as sequential lateral traces or rib traces. The very large glands of *Pithecellobium* obtained a vascular supply from the adaxial bundles of the complex petiole vasculature (Elias 1972).

PHYLLODES

The term phyllode literally means leaflike, and has been applied in plant morphology in a variety of ways to flattened photosynthetic petioles; to rachides of compound leaves which have lost their leaflets; and to a quantity of dissected leaves with terete segments. A flattened leaflike stem may be termed a platyclade, a phylloclade, or a cladode.

The phyllodes of species of *Acacia* may be genetically without leaflets, or in maturation fail to develop leaflets, or lose the leaflets by abscission at various stages of development. Boke's (1940) study of the laterally (vertically) flattened phyllodes of several species of *Acacia* revealed fundamental differences in development, including the dominance of the

adaxial meristem in producing the flattened organ. A short pulvinus was present, as were stipules. The orientation of the vascular bundles simulated the pattern present in the petiole of other leaves. Boke concluded that the phyllode was homologous to a petiole-rachis of a pinnately compound leaf. The initial three vascular traces in the phyllode are supplemented with interpolated bundles. Slade (1952) reported a similar interpolation of traces in cladodes of several New Zealand brooms. Peters (1912) recognized three types of phyllodes in *Acacia* which he termed "Platentypus," "Binsentypus" (rushlike), and "Übergangstypus" (transitional types). Phyllodes in species of *Oxalis*, e.g., *O. fruticosa*, *O. ptychochala*, represent the petiole of a palmately compound leaf which has lost the leaflets in development.

Articulated leaves have been described and illustrated for several families (Troll 1939). The "Gelenkknoten" of *Polyscias* species are clearly in the position of leaflets lost phylogenetically or ontogenetically from terete rachides, since one or more foliage leaflets are present. Species of *Citrus* occasionally show a similar articulated form. Troll (1939) illustrated the articulated phyllode of *Phyllarthron* (Bignoniaceae). Saha (1952) studied *Phyllarthron commorensis* and concluded the "leaves are simple, petiolate with segmented blades." He denied the existence of articulation within a leaf, ignoring the frequent occurrence of such segments in the Bignoniaceae. *Phyllarthron* should be re-examined to determine if it is not a compound leaf which has lost or not developed pinnae.

Kaplan (1970b) has studied the development of the "rachis-leaves" in two genera of the Umbelliferae, and concluded that these terete leaves with septae are the equivalent of the rachis of a pinnately compound leaf with the appendages reduced, transformed pinnae which function as hydathodes.

Terete leaves have often been described as unifacial leaves. A cross section of the leaf may reveal the bundles are arranged in a circle with the phloem of each trace oriented to the periphery. Stomata may have a uniform distribution around the leaf surface, rather than be limited to the abaxial surface as in most dorsiventrally flattened leaves. Flachs (1916) proposed a classification for leaves of plants in the Australian flora which are terete or nearly so, and recognized "äquifacial" (laterally flattened), "unifacial," "bifacial," and "transitional" types. The classification was based mainly on the orientation of the bundles. The abrupt transition from a laminar leaf of *Hakea* (Proteaceae) to the dissected leaf with terete segments is shown by Troll (1939). *Franklandia fucifolia* (Proteaceae) is commonly cited as an example of foliar dichotomous divisions in terete or unifacial leaves.

EPIPHYLLOUS INFLORESCENCES

Flowers may be borne on leaves as single flowers or in inflorescences, and have been described as epipetiulous, epiphyllous, or hypophyllous according to their position; an epiracheal type should be recognized for com-

pound leaves (PLATE VIII). Johnson (1958) has supplied a modern listing of 20 genera in 10 families, to which the Chailletiaceae should be added.

Payer (1890) concluded that the leaf and its axillary flowering branch were fused when flowers were borne epiphyllously. De Candolle (1890), after studying the vascular structure of the petiole and the blade, concluded instead that the epiphyllous inflorescence was of foliar origin. Stork (1956) debated whether the flattened structures bearing flowers might be considered "cladophylls." Melville (1962) regarded the epiphyllous inflorescence as evidence of his proposed primitive "gonophyll."

The hypophyllous inflorescence of *Erythrochiton hypophyllanthus* (Rutaceae) is apparently unique in the Angiospermae in bearing a flower on the lower side of the lamina (Engler 1897). Melville (1962) stated that "above the insertion of the inflorescence there is nothing unusual in the structure of the midrib. Below the flowers, the midrib bundle lies above and quite distinct from the vascular strands supplying the inflorescence. It is evident that in *Erythrochiton* the inflorescence is truly adnate to the lower surface of the leaf." No specimens are available to me for further examination of the vascular supply within the petiole to determine the origin of the traces supplying the inflorescence. Whether these are axillary to the leaf bearing the inflorescence or are from the subjacent node is not known.

Epipetiolar inflorescences are reported at the base of the petiole, along the petiole, or at the apex of the petiole. Johnson (1958) has shown that the epipetiolar inflorescence of *Turnera ulmifolia* originates as a branch trace and becomes associated in the petiole, but is not fused with the vascular supply of the leaf. He concluded that "the epiphyllous inflorescence in *Turnera* is axillary in origin, and through subsequent growth in the foliar buttress is displaced to a petiolar position . . . 10 out of 13 species of *Turnera* examined have epiphyllous inflorescences which originated in the axil of a foliar primordium." Prance (1972) described the vascular patterns in the petiole of several taxa of the Dichapetalaceae in which the inflorescence is borne at various positions on the petiole or well up on the midrib. He recognized "floral bundles" or "inflorescence trace" as distinguishable from "leaf bundles" or "leaf traces" in both sterile and fertile leaves. Although he stated "the floral bundles definitely arise from the leaf bundle within the petiole rather than in the stem" (p. 9), he stated later (p. 12) that "the presence of floral bundles in some sterile petioles, and the separate nature of the floral bundle, demonstrate that the position of the inflorescence has arisen by a gradual fusion of the peduncle with the petiole rather than being a true epiphyllous inflorescence."

Hallé and Delmotte (1973) have illustrated the difference in vascular patterns within the inflorescence axis and the petiole from which the inflorescence arose in the epipetiolar member of the Gesneriaceae, *Epithema tenue*. Regrettably they do not show the relationships of individual bundles, or the origin of the vascular tissue supplying an axillary bud present between the inflorescence axis and the petiole.

Van Steenis (1961) described the "flowers serially bursting forth almost the entire length of the hypocotyl (petiole)" in *Moultonia singularis* (Gesneriaceae), and Letouzey et al. (1969) show several inflorescences arising from the long petioles of *Mocquerysia multiflora* (Flacourtiaceae). No data are given in either case for the vascular structure of the petiole.

Barth (1896) studied various species of the Dichapetalaceae in which petiole-borne inflorescences were present ("fertile leaves") or absent ("sterile leaves"). In the petioles of "fertile leaves" he found a stem-like vascular structure, the adaxial portions of which formed the vascular supply to the inflorescence. Such leaves may also have an axillary bud. In some "sterile leaves" the petioles also had an adaxial vascular supply comparable to that of the "fertile leaves." In others, the petiole had only a simple arc of xylem and a bud in the axil. Additional species were intermediate between the two extremes. Barth accepted the idea that the epiphyllous inflorescence was a congenital accrescence of the petiole with the floral peduncle; and although the bundles were of a foliar origin, concluded that the inflorescence is nothing more than one bud of several which might be produced in the axil. Stork (1956) concluded from his studies that "various degrees of coalescence prevail in species of Dichapetalaceae where inflorescences are borne on the petioles." To Melville (1962) "the sequence of vascular structures to be observed in the Chailletiaceae provides no evidence for adnation . . . but rather, it shows the last stages in the disengagement of the fertile branch from its leaf."

All of the inflorescences borne on leaf blades have been reported for simple leaves with the sole exception of *Chisocheton pohlianus* (Meliaceae), which may bear clusters of flowers in the axils of the pinnae of a pinnately compound leaf. Another species of *Chisocheton* is now known in which a simple or branched racemose inflorescence develops from the rachis of the compound leaf (Peter Stevens, pers. comm.). Harms (1917) illustrated a specimen with flowers borne in the axils of three pairs of leaflets. The illustration also shows an axillary bud at the base of the leaf, and immature pinnae at the apex. Contrasting is another shoot illustrated with an axillary racemose inflorescence and a separate pinnately compound leaf. No anatomical data are offered by Harms on the relationship of the vascular supply of the epirachial inflorescence to that of the rachis and the leaf blades. Melville (1962) refers to a "new species of *Chisocheton*" in which sections of the rachis were cut to reveal a "stem-like structure below the insertion of the inflorescence and leaf-like structure above." Considering the complex vascular patterns found in the rachis of leaves of the Meliaceae, this statement by Melville is unrevealing.

Flowers that are borne on the simple leaf blade are generally associated with the midrib or proliferations of it in pinnately veined leaves. Possible exceptions are found in *Peperomia foliiflora*, in which the inflorescences arise from the base of diverging palmate venation. No material is available for anatomical investigation. Data are also wanting for the epiphyll-

lous palmately veined leaves of *Begonia prolifera* and *Begonia sinuata* cited by Johnson (1958).

The flowers may be at one of several positions along the blade, being near the middle of the length of the blade or along the extreme portions of it, even at the ultimate apex. Letouzey et al. (1969) concluded that the relative position of the inflorescence may vary and is without taxonomic significance. They further explain the presence of a large bract subtending the epiphyllous inflorescence of *Phylloclinium bracteatum* as an example of hyperfoliarization.

De Candolle's (1890) study of the vascular supply to the epiphyllous inflorescences of *Polycardia* (Celastraceae), *Phyllonoma* (Dulongiaceae) and *Helwingia* (Cornaceae) formed the basis for his conclusion that the inflorescences were foliar in origin and not concrescent branches. Melville (1962) stated: "in all of these the vascular system of the petiole, where it left the branch, was an open arc which, further up, arched round and formed a complete circle, as in a stem. . . . In all of these examples where the midrib extends beyond the inflorescence, its trace in section has the open arc appearance, which is very common in angiosperm leaves." Johnson (1958) reached the same conclusion. Watari (1939) was not aware of De Candolle's work, and supported the contrasting idea of Thouvenin (1890) that the traces for the flowering branch were fused with the petiole and the lamina. He cited species of *Saxifraga*, *Chrysosplenium*, and *Vahlia* in which branch traces fuse with the foliar traces in a comparable manner.

With the exception of the study by Johnson (1958) on *Turnera* and *Helwingia*, the majority of the anatomical data available in the literature does not consider the nodal origin of the vascular supply of the epiphyllous inflorescences.

The Dichapetalaceae, Turneraceae, and Flacourtiaceae have trilacunar nodes. The Celastraceae has a unilacunar node. *Helwingia*, variously assigned to the Cornaceae, Helwingiaceae, or Araliaceae, has a unilacunar node, an exceptional pattern in the Cornaceae and most unusual in the Araliaceae where Melville (1962) associates the genus. *Phyllonoma* has been placed in the Saxifragaceae, which has trilacunar or unilacunar nodes, but it is now associated with the Escalloniaceae (Melville 1962) with unilacunar nodes, or as the monotypic Dulongiaceae (Willis 1966). *Phyllonoma* is reported by Stork (1956) to have stipules, and is the only genus with stipules and an epiphyllous inflorescence.

SUMMARY AND CONCLUSIONS

The extreme morphological diversity represented in the photosynthetic organ of extant plants makes impossible a simple yet inclusive and satisfactory definition of either a leaf or a node. The search for this simple definition has resulted in the undesirable distinction made of a leaf and of a stem when these must be recognized, developmentally and morphologically, as a continuous system. The existing statements on the primitive

type of leaf or the primitive type of node are equally futile exercises in semantics. The ancestral forms of the modern "leaf" are either lacking or have not been recognized.

The two basic theories proposed for the origin of the leaf recognize a stem as a primary structure, and the leaf as (1) an enation or protuberance from a stem, which has attained a vascular supply from the stem, or (2) the modification in various ways of a stem or a stem system. Casimir de Candolle (1868) proposed that the leaf was a flattened stem, a stem in which the adaxial portion had atrophied. Agnes Arber (1941) concluded that the "leaf is a partial-shoot . . . revealing an inherent urge toward becoming a whole-shoot, but never actually attaining this goal, since radial symmetry and the power of apical growth and self-reproduction are curtailed or inhibited." The telome theory (Wilson 1942) also proposed a primitive stem system of terete axes with dichotomous branching, from which a flattened leaflike structure could be derived by the fusion of axes (see Croizat 1973, footnote 84) or by the broadening of an individual axis. Such broadening and expansion has been called foliarization, planification, hyperfoliarization, or hypocladiation. Melville's gonophyll hypotheses (1962) are but variations on this theme.

Sinnott and Bailey (1915) concluded that the primitive angiospermous leaf was simple, palmately veined, probably three lobed, and associated with a trilacunar node, but did not consider how this originated. Corner (1949) also begged the question by suggesting that the primitive leaf was a pinnately compound massive structure. He derived smaller and simple or palmate leaf types by reduction.

Some contrasting theories of the origin of the leaf place emphasis on the potential development of portions of a meristematic zone. Primordia in such an area can develop individually, or several can develop in association. The segmentation of the developmental area can produce either a vascular cylinder and a "leaf-skin," or contrastingly a "leaf base" and an apical region (Unterblatt *versus* Oberblatt), with each area of the two approaches having a potential for subsequent recognizable and different diversification.

The primitive node from the trace-gap point of consideration has been proposed variously as trilacunar with single traces (Sinnott 1914); trilacunar with a double trace in the median gap (Takhtajan 1969); unilacunar with a single trace (Benzing 1967); unilacunar with a double trace (Marsden & Bailey 1955), or multilacunar (Ozenda 1948). Associations of these nodal types with floral or other familial characteristics do not reveal any substantial correlation. The so-called primitive floral types may be found with either the proposed most advanced or the proposed most primitive nodal types, while advanced floral types have a preponderance of advanced nodal types but may also be associated with the proposed primitive nodal types.

The general tenet (Smith 1967) that primitive leaves are simple and advanced types of leaves are variously compound also lacks substantiation. The distinctions between a simple and a compound leaf, whether

pinnate or palmate, are either difficult or arbitrary. Gradients do exist also between microphylls and megaphylls, and between sessile and petiolate leaves. The internal structure of any one type can be simple or complex. The proper phylogenetic position of the characteristics of cortical vascular systems and medullary vascular systems has not been determined, but in the majority of cases these unusual anatomical characteristics are associated with simple leaf types.

The evolutionary progress from alternate and spirally arranged leaves to opposite or whorled leaves has become established as a dictum in most botanical publications (Smith 1967, Cronquist 1968) without any real evidence. Only Croizat (1960) has proposed the alternate point of view that "what was originally verticillate of the foliation has tended to be dirempted into sets of leaves, and finally the sets themselves of leaves have . . . been dirempted again into single leaves in accordance with alternate and spiral modes of foliation."

A solution to the problem of what is primitive and what is advanced may well necessitate the abandonment of modern botanical semantics, and especially the current concepts of the leaf as a fundamental structure or a unit of the plant. The "leaf" of our current thinking may well have multiple possibilities of origin.

Croizat (1973) has proposed seven possible means of origin of the "leaf," and recognizes that there may be more. He suggests the following: 1. A simple scale (leaf *sensu stricto* of *Asparagus*). 2. An inflorescence adapted and imperfectly developed (leaf-cladode of the *Asparagae*). 3. An inflorescence adapted and imperfectly developed and joined with abundant fused fibers (*Washingtonia*). 4. A "rama-stem" of second or third order with characters more or less foliaceous (*Phyllanthus*, *Schumanniophyton* and *Guarea*, *Chisocheton*, *Schizolobium*). 5. A scale ("Unterblatt") associated with a primordium which is the origin of the typical "rama" or petiole ("Oberblatt"). This, Croizat remarks, is the typical leaf of the Angiospermae. 6. A leaf formed of fused leaflets (*Bauhinia*). 7. A spathe without a spadix (Araceae). He concluded "these examples do not pretend to be complete, irreproachable, etc. Finally they serve only for orientation and to give a very general idea of the different origins of the leaf. In total the leaf is an organ of complex morphogenetic and phylogenetic origin."

Various authors (Lignier 1888, Morvillez 1919, Maekawa 1952, Croizat 1960) have in the past suggested that the modern leaf is a compound structure, an assembly of components, and not necessarily derived by simple modification of a branch or a stem. Further support of this possibility is in the information on the node and the petiole just presented.

Three aspects of the foliage of the modern dicotyledonous angiosperm require consideration basic to any speculation on the origin of the "leaf."

1. The "node" of the modern dicotyledonous angiosperm is a locus of meristematic activity capable of producing one or more products. These products can be variously associated in development, and each is capable of achieving various degrees of specialization.

The nodal locus may extend around the stem at a given level and have, as well, varying degrees of vertical extension. The evolutionary progress of the nodal locus has been one of spatial restriction in toto as well as in the specialization of its derivative products. The products of the meristematic activity of the nodal locus, as has been pointed out, may be the leaf, occurring alternatively as a scale, a prophyll or an eophyll; stipules; vegetative or floral buds; vascularized or unvascularized glands, etc.

Applicable here are the studies of sheathing stipules which suggest that the nodal locus, as a meristematic zone, is capable of development completely around the stem, with a portion of the derivative tissue specialized into a foliage leaf, and the other portions existing as the sheathing stipule. It should be noted that the stipular portion may be free of the leaf in a lateral position, adaxial to the leaf, opposing the leaf, or located above or below the leaf. Since there are examples of the vascular independence of the leaf and the stipule, the stipule should be considered, in some cases at least, not a portion of the leaf, but phylogenetically a structure equivalent to the leaf where both may be developed from the same nodal locus meristem.

2. The leaf may well be a compound structure assembled by the lateral association of primordia from the nodal locus meristem developing individually or collectively. It has been pointed out that within the petiole and/or the complete leaf the several vascular bundles may be independent. It is possible to recognize the individuality of vascular bundles in many leaves. The median trace, for example, is most easily recognized and may extend undivided and unbranched to the uppermost portion of the leaf blade before developing secondary venation: i.e., the median trace, when more than one trace is present, vascularizes the upper portion of the leaf blade. Likewise, the median trace may be present only in the base of the petiole, and may deteriorate or be lost in the petiole or the blade. The lower portion of the entire leaf blade, or in some cases the lateral basal lobes of the simple leaf may be vascularized only or primarily by traces which enter the stem as lateral traces.

In many dicotyledons the median trace may give rise in the base of the petiole to two branches which assume an adaxial position. These adaxial branches of the median trace may fuse or remain independent to the tip of the blade. Lateral traces from the stem may then be interpolated in the petiolar vascular tissue between the median trace and its derivative adaxial branches. The secondary venation of the lower portion of the leaf blade may be derived only from these lateral trace components, and the lateral traces may be completely used up in the lower portion of the leaf blade, with the upper portion of the blade being supplied vascular tissue from the median trace and its adaxially located branches.

The path of derivative bundles from the cortical vascular system or the medullary vascular system of the stem within the petiole and the leaf blade also suggests the "leaf" is an assembly. The cortical vascular system within the stem may at times be associated with the principal vascular system or be completely independent of it. Within the leaf,

the derivatives of the stem cortical vascular system may contribute the bundles normally called "laterals" in the petiole, and these extend, clearly recognizable and independent, into the lower portion of the leaf blade.

The medullary vascular system of the stem may also be associated at times, or in some plants, with the principal vascular system, or be independent of it. The medullary bundles of the stem may contribute to the vascular supply of the leaf completely independent of the vascular tissue derived from the principal vascular system of the stem. Within the leaf, the bundles derived from the medullary vascular system of the stem remain in a medullary position in the petiole or the midrib, and do not appear to contribute to the vascularization of the lamina.

The double leaf trace of *Ascarina* described by Swamy (1953) was said to have the two bundles associated with independent parts of the "eustele" of the stem. Within the leaf, each bundle was associated with one half of the lamina by branching only in one direction. Neither Bailey nor Swamy speculated that this might be the fusion product of two ancestral primordia.

Although many examples of interconnections between traces within the petiole, the rachis, or the lamina are known, still the independence and individuality of the trace predominates, and is discernible until secondary activity may obscure the condition. Thus there is much evidence that the leaf is a compound structure, assembled from parts represented today by the distinctive traces.

3. The "leaf" may be compound in the sense of a serially articulated structure, but the significance of the evidence is still not clear.

De Candolle (1868) suggested that the leaf was composed of a linear series of "metameres," and evidence for this is found in the pulvinal areas of the leaf. In compound leaves, one to many pulvinal areas may be present within the length of the leaf, and these may or may not be zones of abscission or articulation. In simple leaves, the pulvinal area may be at the base of the petiole or at the apex of the petiole, or in both locations. Whether or not abscission occurs in the pulvinal area, there is an alteration of the pattern of vascular tissue contrasting with that of the intervening zones. Leaves which lack obvious pulvini may have internal areas of vascular tissue specialized as cross zones at the apex or the base of the petiole, separating otherwise distinctive and characteristic areas of vascular organization.

Strey (1973) has recently described the leaves of *Cussonia spicata* (Araliaceae) where a palmately compound leaf has the segments pinnately compound. He used the terminology of Mirbel (1815) in referring to these leaves as "vertebrate," recognizing the ultimate abscission of each portion of these serially articulated segments. The presence of an apical gland (Cusset 1965) or food body, the so-called Beltian bodies, may also represent examples of metameres and the serial articulation of the leaf. Developmental studies of the serially articulated leaf appear to be completely lacking.

The origin of the modern leaf is to be sought in a small terete structure, probably an enation, with a single vascular strand. The primitive leaf may have developed laterally subsequently in some cases through the action of a marginal meristem. In other cases several of these enations developed as a single unit, the leaf, from the many enations present in the primitive broad nodal plexus of meristematic activity. The primitive leaf was probably borne in whorls or even vertically grouped clusters, and progress was the reduction, enlargement, and isolation of the derivative products. The primitive large nodal plexus has become restricted to the modern leaf scar. Vertical restriction, division, or isolation is recognizable by the development of the internode. Specialization of the derivative products is revealed as stipules, buds, glands, and leaves. It is suggested that areas within the primitive nodal plexus retained a meristematic potential for growth and differentiation, while other areas lost this potential to varying degrees. The multilacunar node of modern plants with a sheathing stipule may well be the residual expression of the primitive meristematic nodal plexus.

Two morphogenetic trends from this nodal plexus should be recognized as rameal and foliar, occurring simultaneously or in varying sequences, thus accounting for the modern pulvinus, petiole, rachis or serial articulations. The number of primitive enations may be represented in the modern leaf by the number of bundles present either in the gap-trace area or in the petiole.

Attempts to place in a single phylogenetic sequence the nodal gap-trace area; alternate, opposite, or whorled leaves; simple or compound leaves; sessile or petiolate leaves; stipulate or exstipulate leaves, etc., are fundamentally useless. Such characteristics of modern plants must be recognized as mid-points in the evolution of the modern leaf. The chances are that such morphological expressions are not sequential, but parallel developments from a very simple ancestral type. The success of the "leaf" as a photosynthetic organ has permitted if not contributed to the great diversification of form in modern foliage leaves.

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EXPLANATION OF PLATES

PLATE I

Examples of nodal patterns. FIGURE 1. a-i. Leaves alternate: a. one trace; b. two traces from one gap; c. three or more traces from one gap; d. alternating traces to the leaf and an axillary bud in *Euptelea*; e. single trace showing vascular supply to stipules; f. three traces from three gaps; g. lateral traces of a trilacunar node with vascular supply to stipules; h. multilacunar node without stipules; i. multilacunar node with lateral traces showing vascular supply to the sheathing stipule.

FIGURE 2. a-f. Leaves opposite: a. one trace from each gap; b. two traces from each gap; c. three (or more) traces from each gap; d. opposite trilacunar nodes; e. "common gap" or "split lateral" condition where vascular supply of lateral traces to each of opposite leaves is supplied from a single lateral gap; f. a "split lateral" condition with two traces in each of the median gaps.

FIGURE 3. a, b. Leaves whorled: a. one trace from each gap; b. trilacunar condition with three traces from three gaps to each of three whorled leaves.

FIGURE 4. a-h. Examples of cortical bundles: a, c, e, g are internodal sections; b. the cortical bundle enters the leaf and is replaced in the suprajacent internode by a bundle derived from the central vascular cylinder; d. a "split lateral" with divided cortical bundles, of which one portion enters the leaf and the other continues in the stem; f. stem cortical bundles divide with portions of each entering the leaf and a portion continuing in the stem (a girdling nodal trace may also connect the cortical bundles); h. alternate leaf arrangement with two of the cortical bundles dividing to supply vascular tissue to each leaf.

PLATES II-IV

Diagrams of selected petiole vascular patterns. Successive sections were taken at the leaf base, the middle of the length of the petiole, and at the apex of the petiole or the base of the blade before the departure of the secondary veins. In FIGURES 1 to 4, the leaves may be alternate, opposite or whorled, simple or compound, with or without stipules. The stem may have, or lack, cortical and/or medullary vascular systems. See text pp. 144-150 for further explanation.

PLATE II

FIGURE 1. a-j. Nodes with one trace from one gap. FIGURE 2. a-e. Nodes with two or three traces from one gap.

PLATE III

FIGURE 3. a-n. Nodes with three traces from three gaps.

PLATE IV

FIGURE 4. a-d. Nodes with three traces from three gaps. FIGURE 5. a-e. Multilacunar nodal types with five or more traces from an equal number of gaps; leaves alternate only, but stipules may be present or absent.

PLATES V-VII

Examples of selected sections of stems, petioles, and laminae showing the continuous vascular patterns of different taxa. Diagrams produced from camera lucida drawings and, excluding the outline drawings of the leaf, the nodal and petiole sections for each taxon are on the same scale. Sclerenchyma tissue is shown in heavy black lines.

PLATE V

FIGURE 1. a. leaf of *Banksia serrata* (Proteaceae); b. section of trilacunar node; c. middle section of short petiole, median trace has produced two adaxial bundles while laterals divided many times, first veins depart from center of series of branches of the laterals; d. base of blade, similar organization of bundles but each surrounded by ring of sclerenchyma.

FIGURE 2. *Hakea dactyloides* (Proteaceae): a. leaf; b. node; c. petiole lacking adaxial derivatives of median trace and single division of lateral traces, all embedded in heavy sclerenchymatous tissue; d. section of leaf, veins are the lateral traces, and median trace has divided for the first time.

FIGURE 3. *Coccoloba rugosa* (Polygonaceae): a. leaf with sheathing stipule; b. subjacent nodal section showing precocious origin of traces; c. nodal section, upper traces enter stipular sheath, median and laterals enter petiole; d. basal section of petiole showing divergent trace branches in the "cross zone," note the absence of sclerenchyma in the lower pulvinal area; e. midpetiole section showing the organization of vascular bundles in several concentric rings; f. base of leaf blade with the organization of an adaxial plate from several lateral bundles.

FIGURE 4. *Amphilemma cymosum* (Melastomataceae): a. leaf; b. internodal section showing medullary bundles; c. nodal section showing path of medullary bundles or their branches into the leaf base; d. mid-petiole section with medullary bundles from the stem in a medullary position; e. section through midrib with medullary bundles still present.

PLATE VI

FIGURE 1. *Symplocos glauca* (Symplocaceae): a. leaf; b. nodal section; c. section at base of petiole; d. section in middle of petiole, the rib-traces having arisen from the ends of the vascular tissue; e. midrib section.

FIGURE 2. *Peperomia hernandiifolia* (Piperaceae): a. peltate leaf; b. nodal section showing "herbaceous" pattern of scattered bundles, three traces from three "gaps"; c. base of petiole, lines separate the products of the three traces; d. upper end of petiole at attachment to peltate blade, bundle in medullary position supplies central veins descending from midrib, upper two bundles on each side supply basal veins of leaf, median and its branches supply vascular tissue for the upper portion of the blade.

FIGURE 3. *Melicoccus bijugatus* (Sapindaceae): a. leaf showing broadened rachis below upper leaflets; b. nodal section; c. base of petiole; d. terete portion of petiole below first pair of leaflets; e. section at the point of attachment of basal pair of leaflets; f. section at point of attachment of upper pair of leaflets; g. section of petiole of a leaflet.

FIGURE 4. *Aesculus hippocastanum* (Hippocastanaceae): a. palmately compound leaf; b. base of petiole, bundles may have originated from tri- or pentalacunar node; c. pulvinal section of petiole; d. just above the pulvinus two branches from median trace assume a medullary position; e. middle of petiole; f. apex of petiole at point of attachment of leaflets, medullary bundles of previous section have resumed association with median trace and its branches; g. section of petiole of leaflet.

PLATE VII

FIGURE 1. *Sloanea dentata* (Elaeocarpaceae): a. leaf showing upper and lower pulvini of petiole; b. nodal section; c. supranodal section showing dorsal association of lateral traces; d. section of lower pulvinus; e. section from middle of petiole, invagination and foldings have produced a medullary ring shown with a surrounding layer of sclerenchymatous tissue and dorsal small bundles each with ring of sclerenchyma; f. dissociation of heavy vascular rings in the

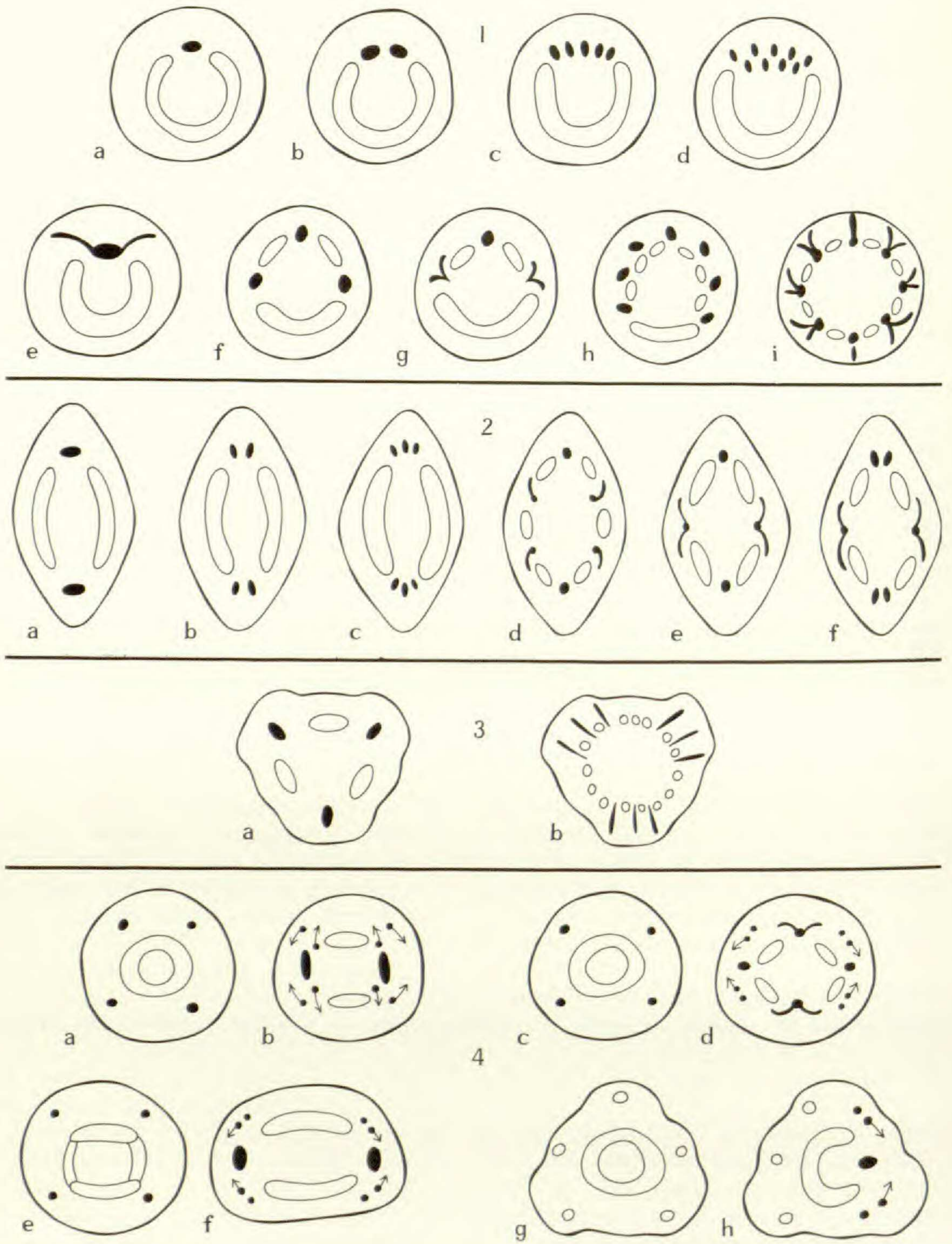
upper pulvinus, dorsal bundles have departed to lower veins; g. midrib section at point of first strong secondary veins.

FIGURE 2. *Populus tremuloides*: a. leaf, flattened petiole not well depicted; b. nodal section showing patches of scattered sclerenchyma; c. base of petiole; d. lower portion of petiole; e. middle of the petiole showing the organization of the vascular supply into a series of "rings"; f. apex of the petiole; g. base of the blade, middle bundles of the flattened portion of the previous section supply the basal secondary veins.

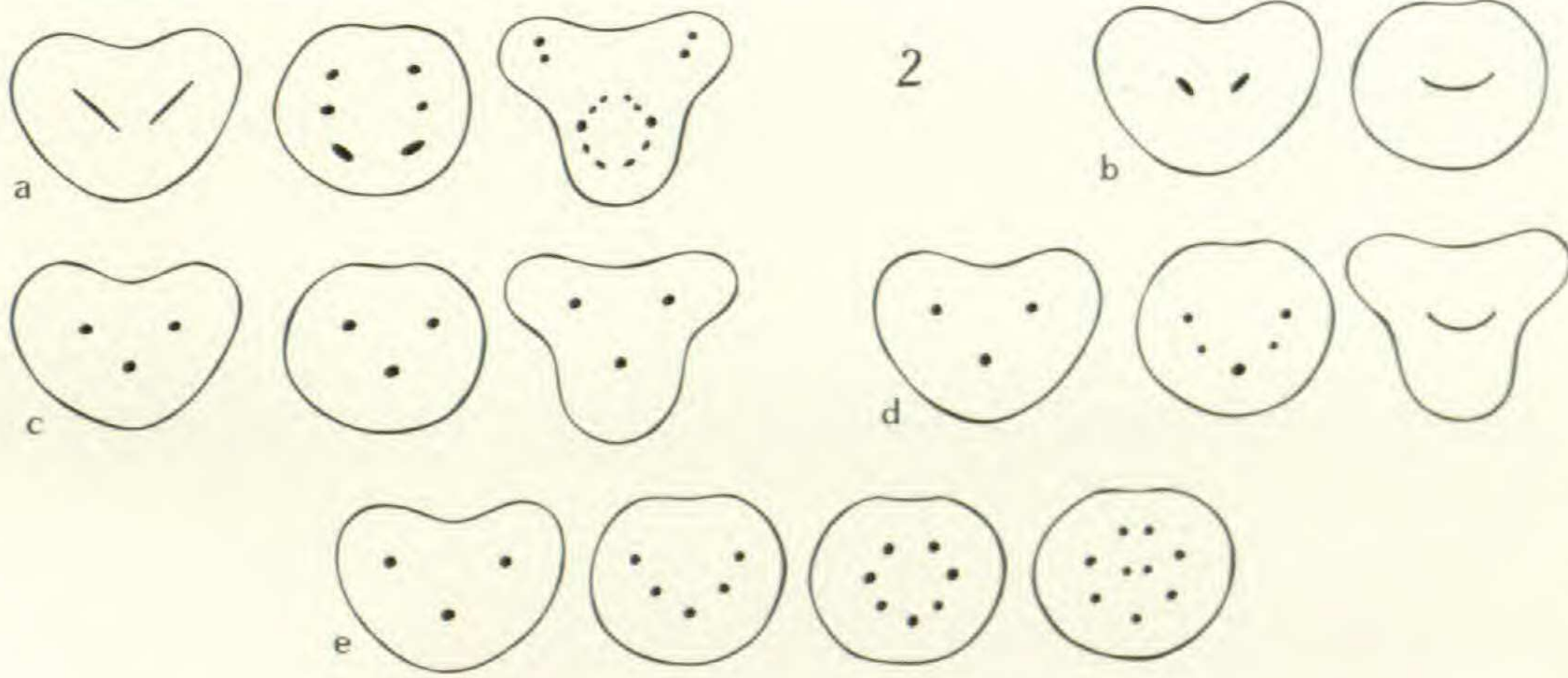
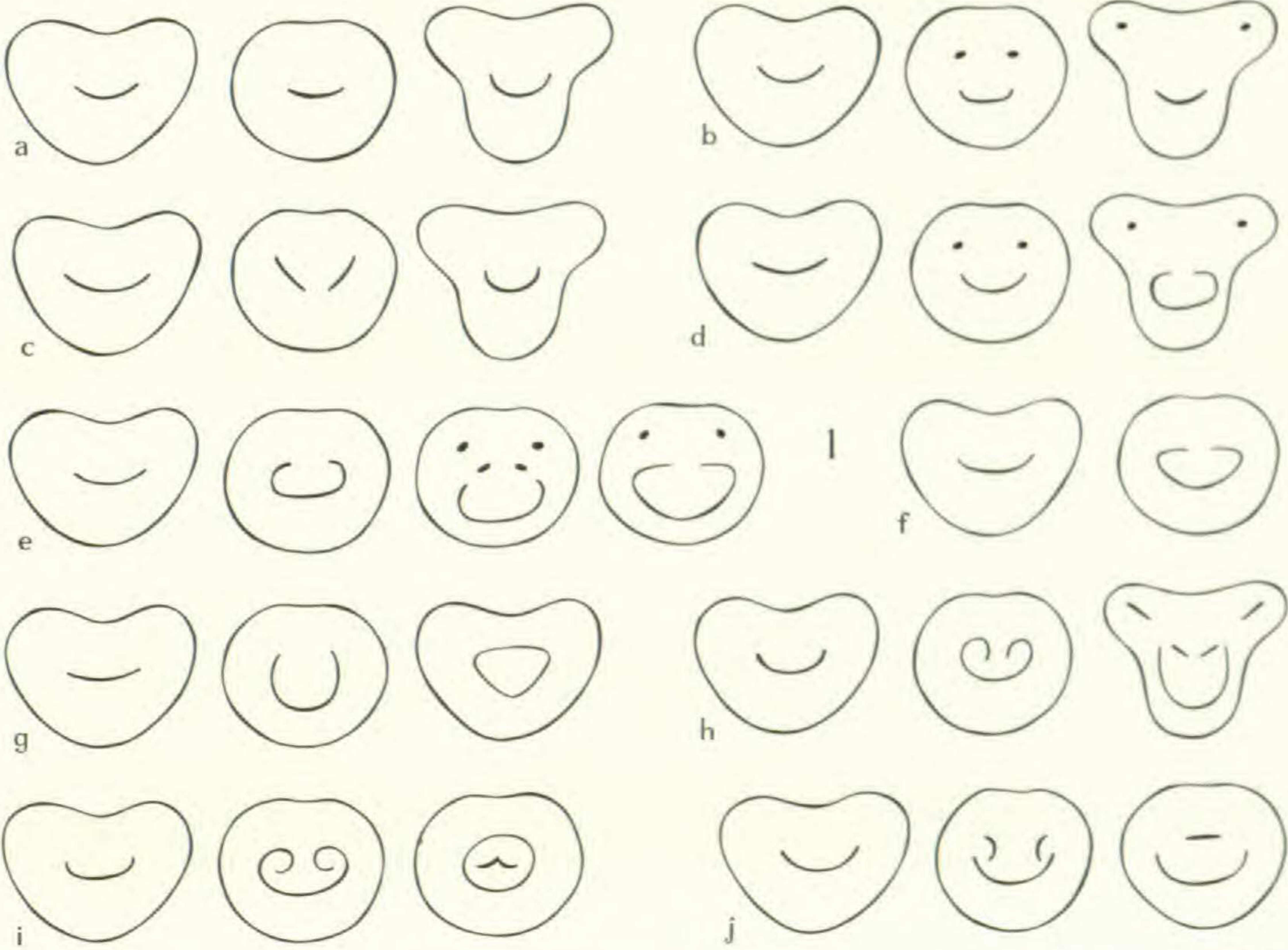
FIGURE 3. *Aristolochia esperanzae* (Aristolochiaceae): a. leaf; b. nodal section showing the distinct bundles of the stem; c. middle of the petiole showing the median bundle, two division products of each lateral trace, and the heavy sclerenchyma layer; d. base of leaf blade with the departure of the basal veins.

PLATE VIII

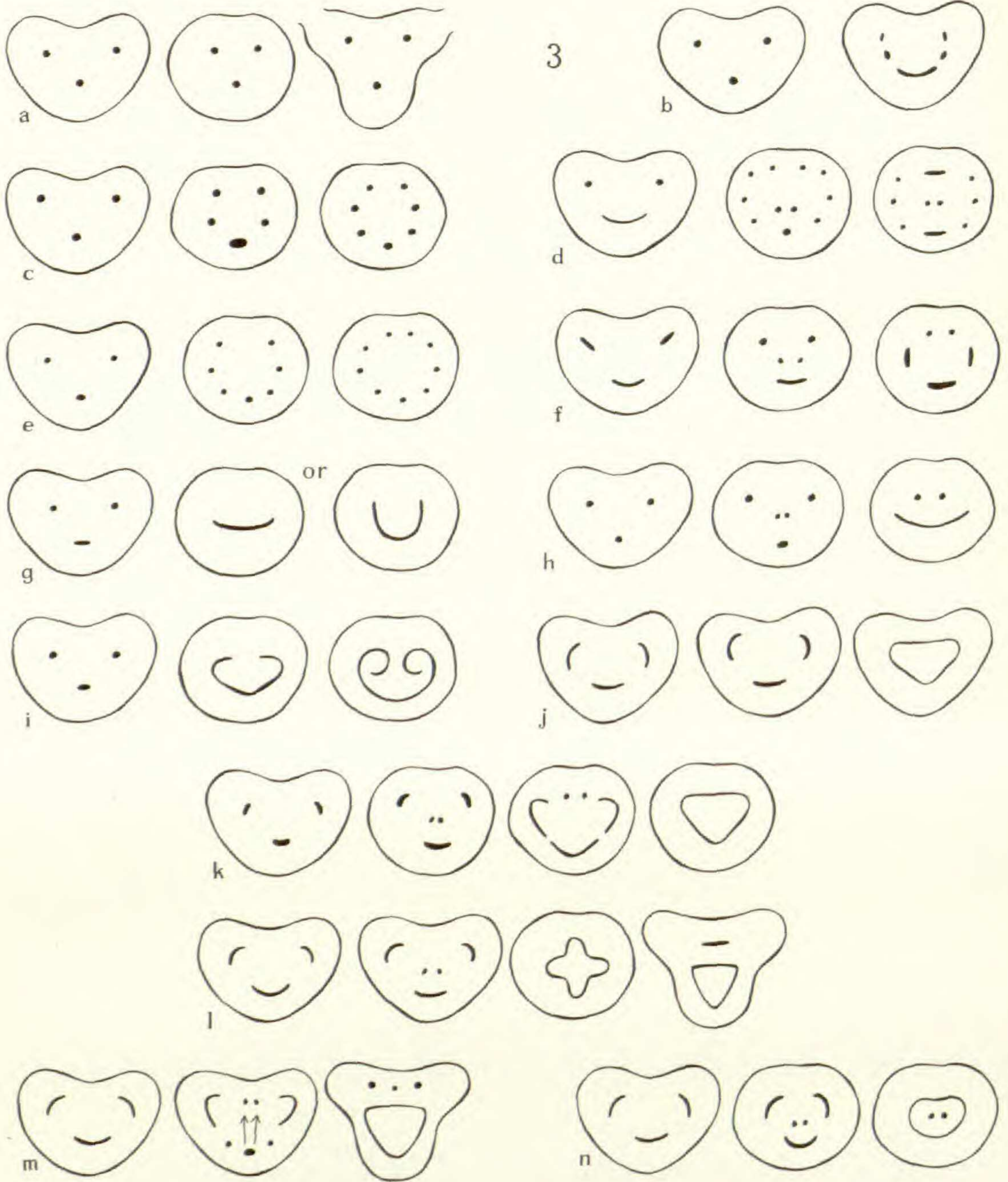
Examples of epipetiolar, epiphyllous, epirachial, and hypophyllous inflorescences. Scale marker is 1 cm. a. *Dichapetalum latifolium* (Dichapetalaceae), inflorescences from petiole; b. *Helwingia japonica* (Cornaceae), epiphyllous cluster of flowers, plants dioecious; c. *Phyllonoma laticuspis* (Dulongiaceae), epiphyllous inflorescences; d. *Turnera ulmifolia* (Turneraceae), single flower with bracts borne on the petiole; e. *Chisocheton pohlianus* (Meliaceae), epirachial flowers and racemes from single pinnately compound leaf; f. *Polycardia phyllanthoides* (Celastraceae), terminal epiphyllous flowers; g. *Phyllobotryum spathulatum* (Flacourtiaceae) [redrawn from Hooker's *Icones* 14: *Plate* 1353. 1881, and herbarium material], flowers borne on upper surface of midrib, (epiphyllous); h. *Tapura latifolia* (Dichapetalaceae), flowers borne here at apex of petiole, but may also be on the lamina; i. *Erythrochiton hypophyllanthus* (Rutaceae) [redrawn from Engler, Engler & Prantl, *Nat. Pflanzenfam.* III. 4: 96. *fig. 96 F.* 1896], flower borne on abaxial surface of lamina (hypophyllous).



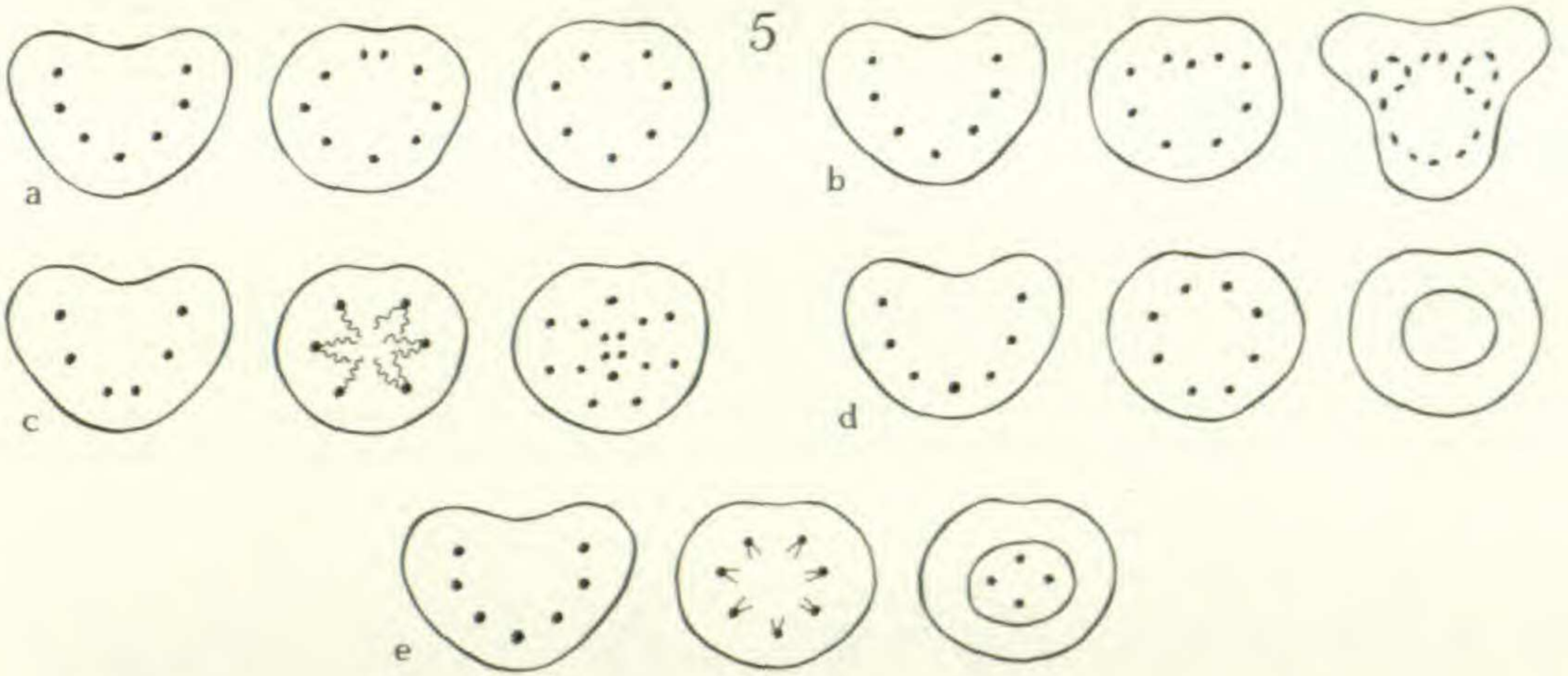
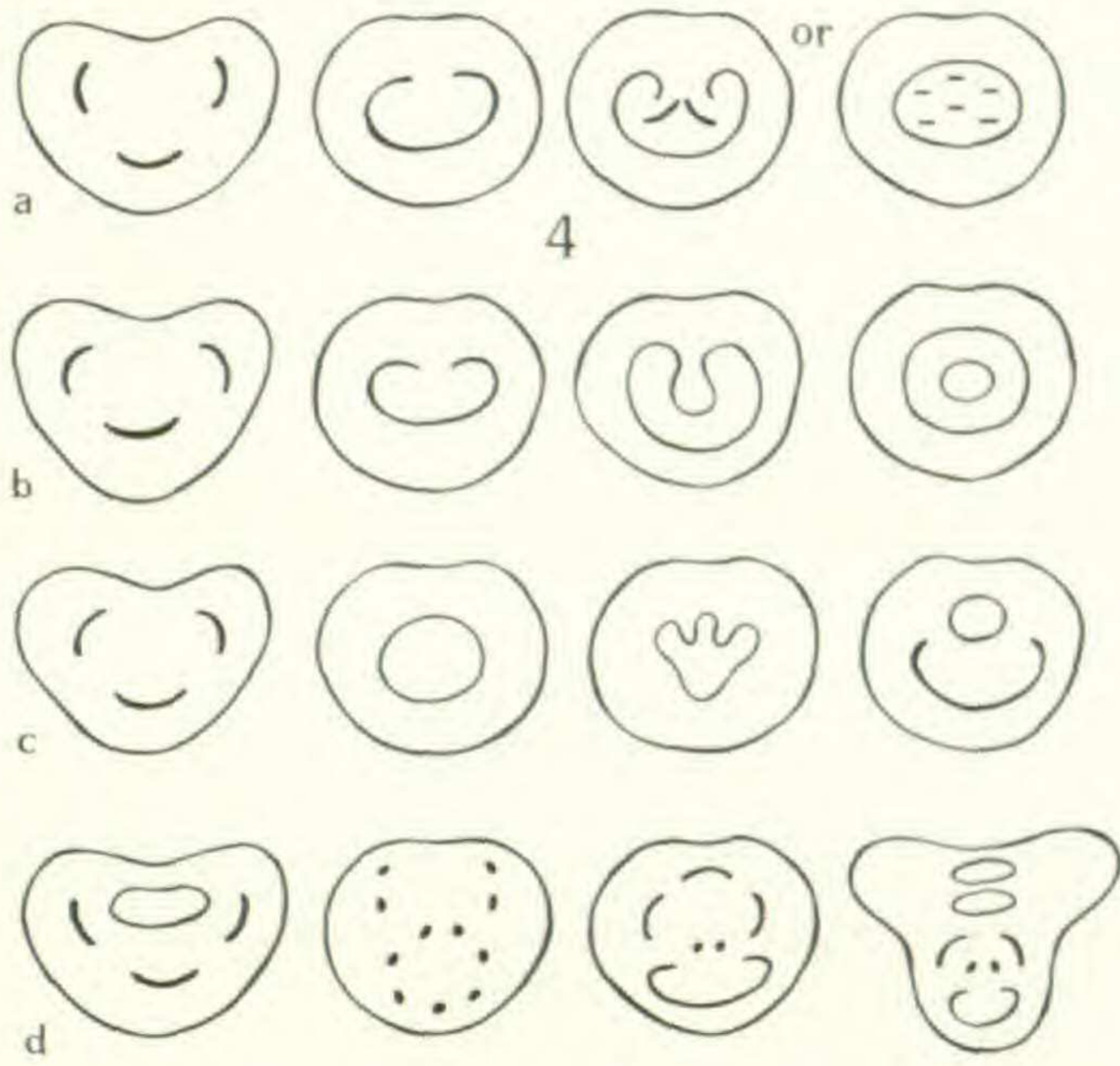
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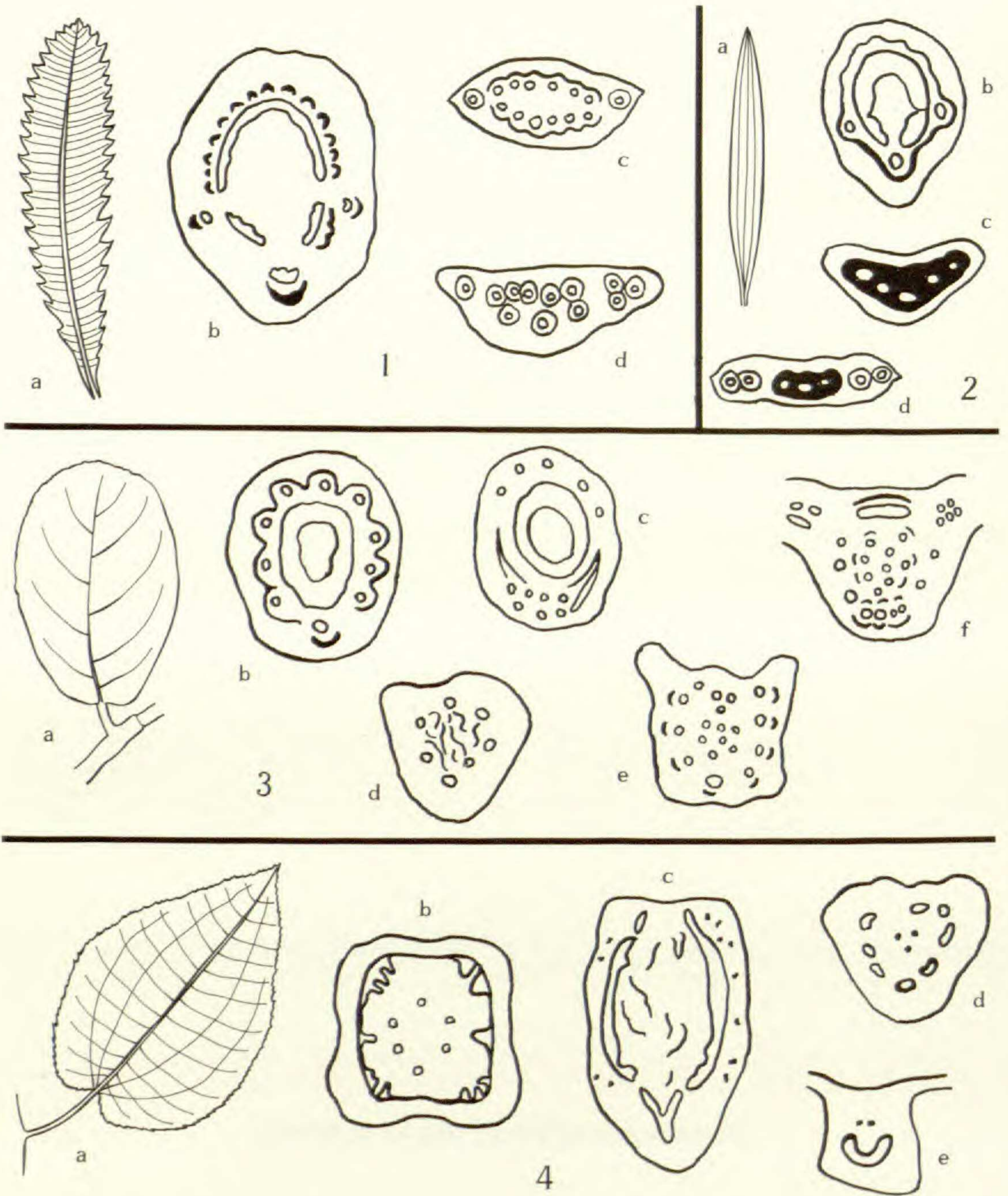
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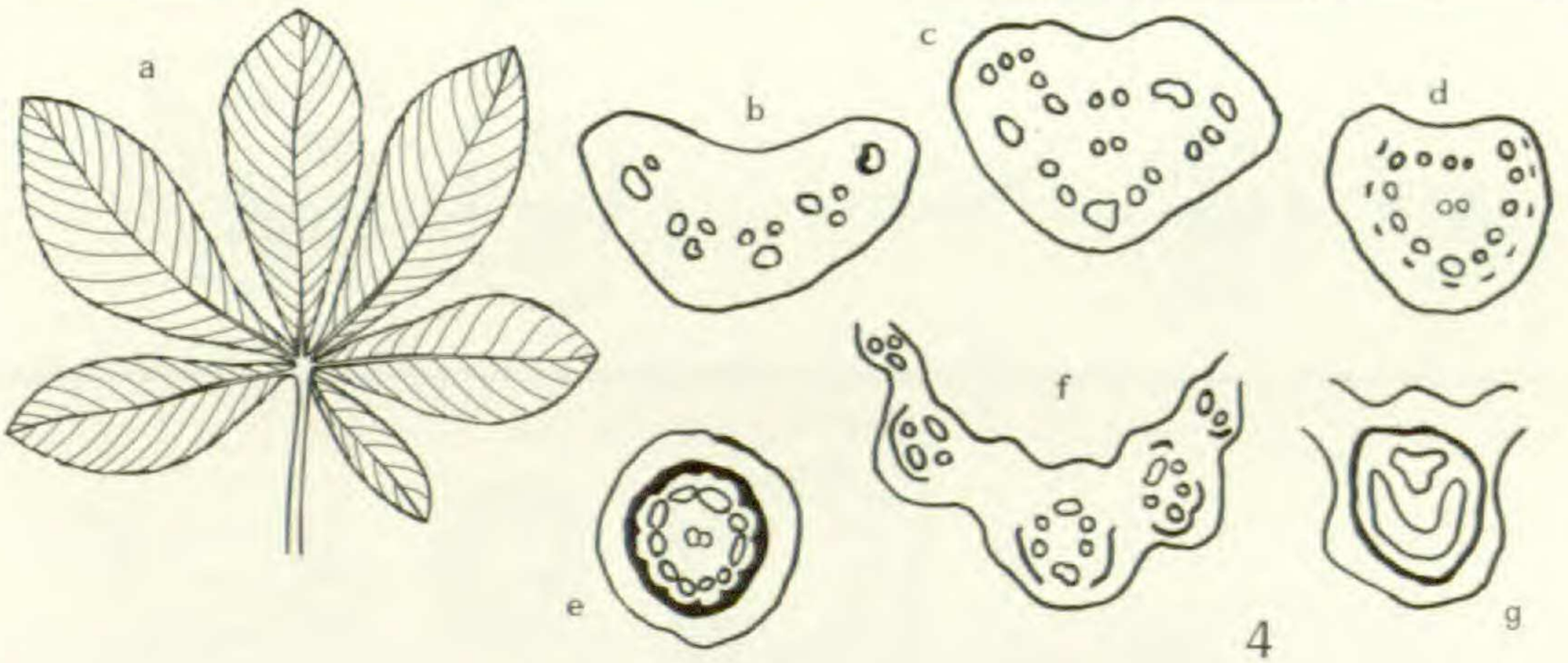
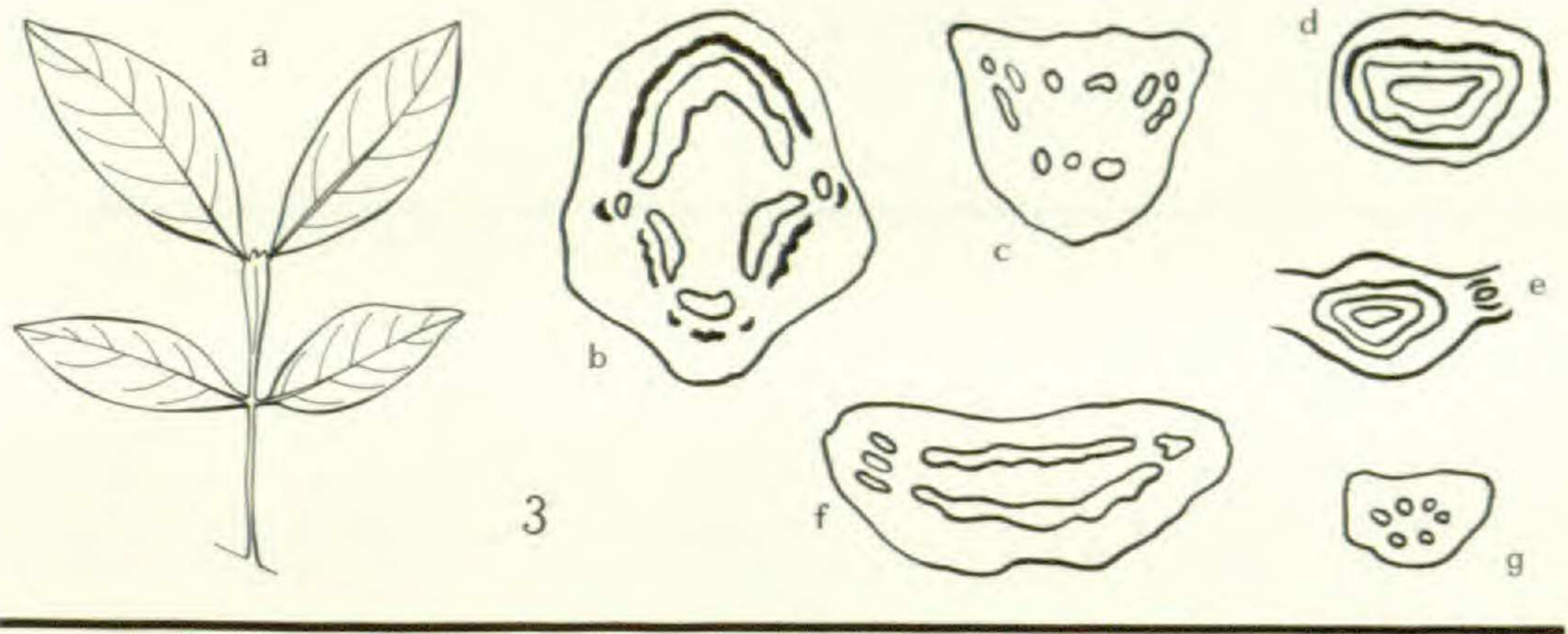
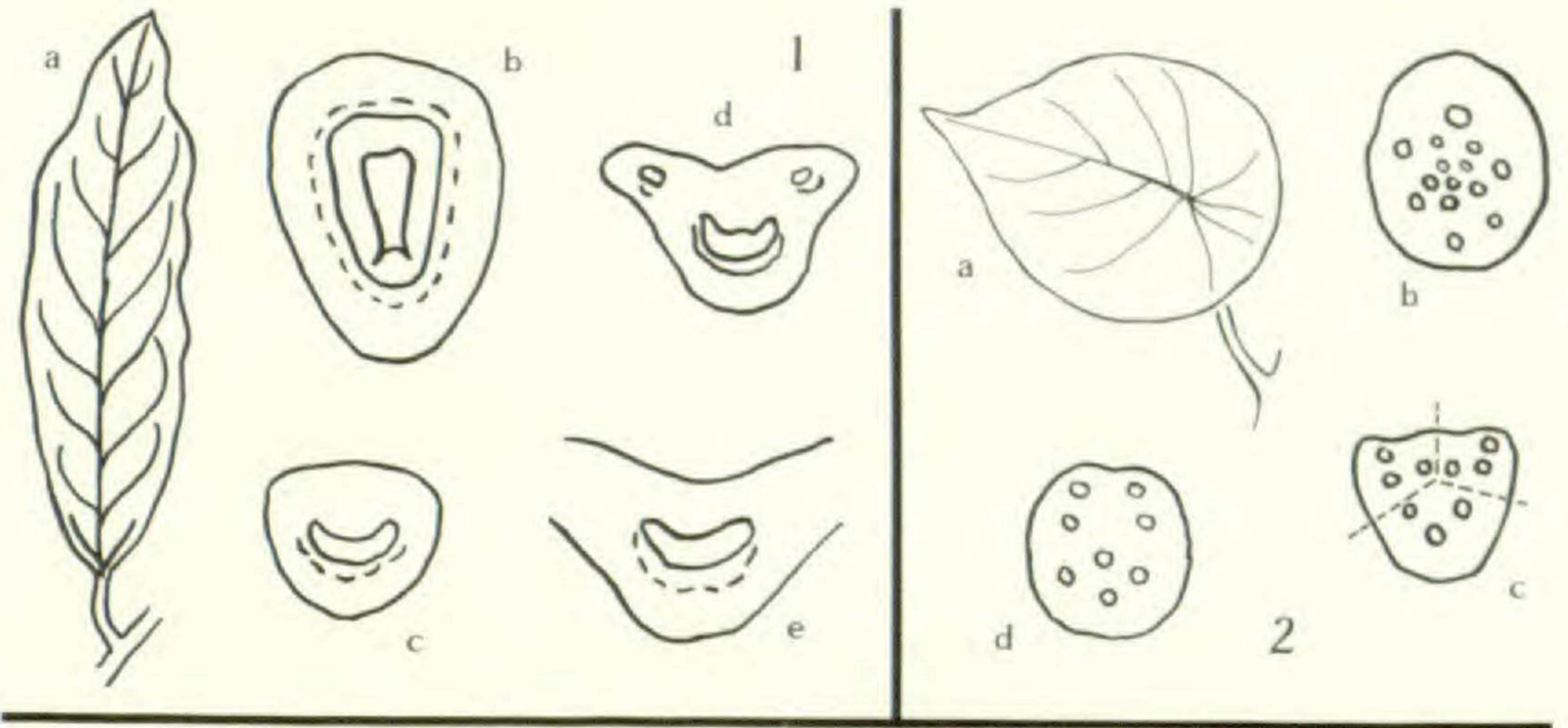
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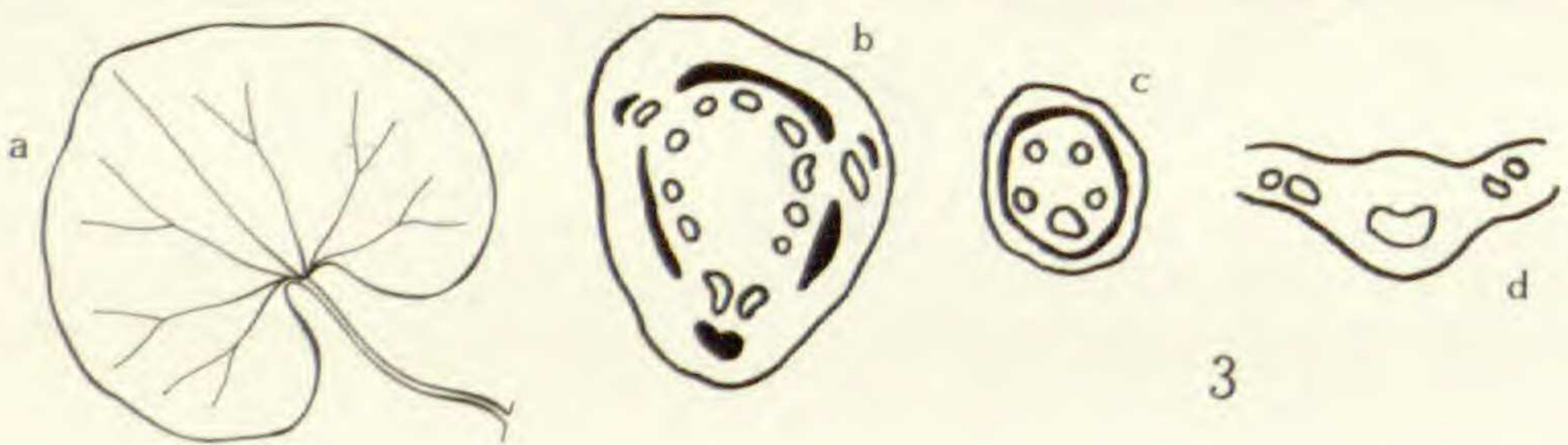
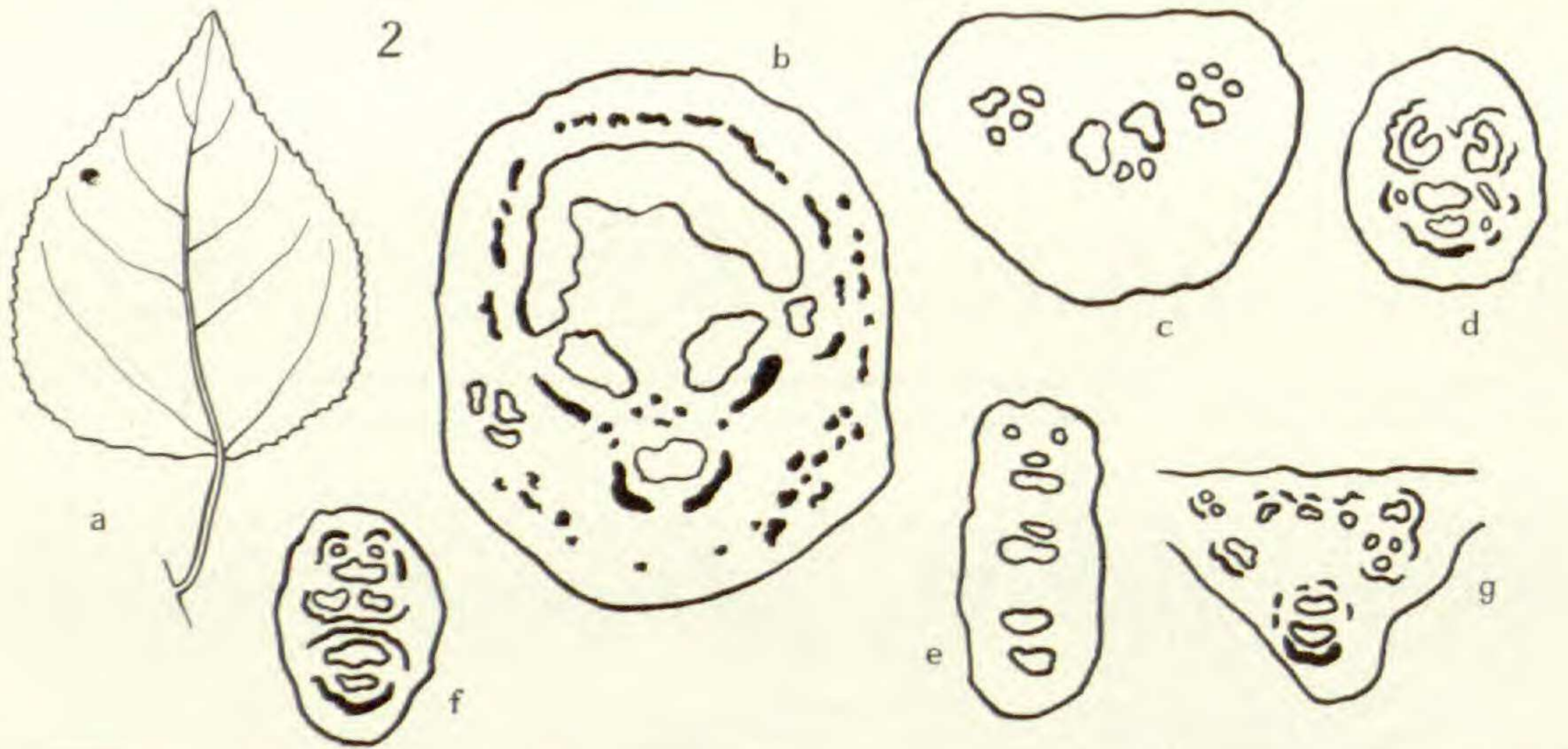
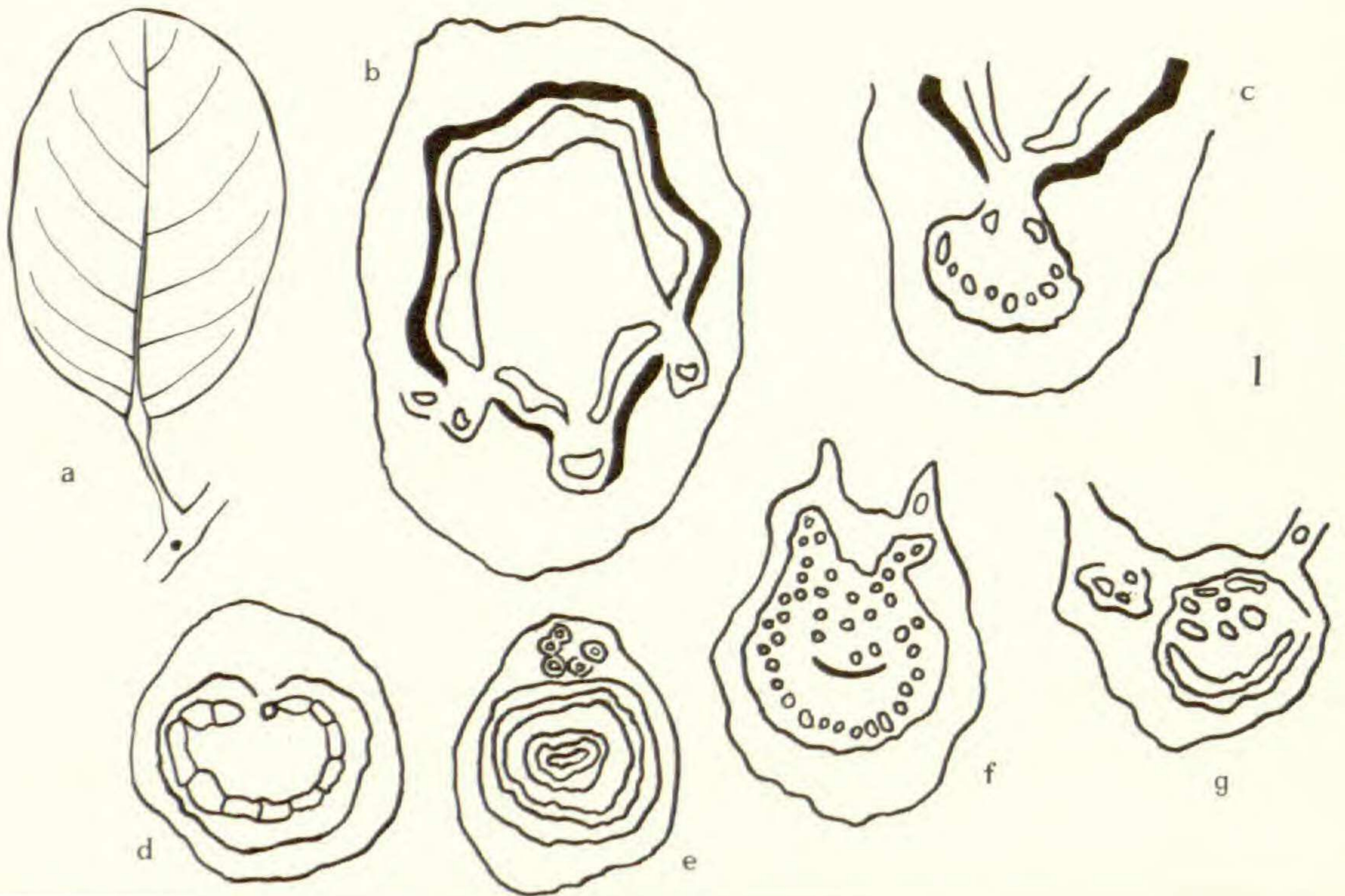
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